MIGRATION PATTERNS AND ENERGETICS OF ADULT CHINOOK SALMON *ONCORHYNCHUS TSHAWYSTCHA* IN ALASKA RIVERS

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Abstract

Adult Chinook Salmon *Oncorhynchus tshawytscha* undertake extensive and energetically costly migrations between food resources in the ocean and their freshwater spawning habitats, requiring them to adapt behavioral and physiological traits that allow them to successfully reach their spawning streams and reproduce. Such adaptations may be shaped by physical factors in the environment and individual- and population-specific biological characteristics. Chinook Salmon in North America are important resources for both United States and Canadian stakeholders, but relatively little is known about their freshwater migration patterns and energetic status in many rivers across their range. This research explored variation in migration timing and migration rates of Chinook Salmon in two Southeast Alaska transboundary rivers (Taku River, Stikine River), examined energetic status at multiple sampling locations in Alaska, and created and tested a predictive model for energetic status using bioelectrical impedance analysis (BIA). Migration timing was earlier for fish that spawned in more distant tributaries in both transboundary systems and the Taku River was earlier compared to the Stikine River. Migration rates decreased during periods of high flows, were slower for fish in the Taku River, and were slower in both systems in 2016 compared to 2015. Migration rates were faster for fish with spawning sites farther upstream when compared to those that spawned closer to the river mouth, but these rates decreased over time as fish swam farther upriver. Chinook Salmon ($N = 129$) sampled for energetic status at the beginning of their freshwater spawning migration had higher total percent lipid than those near the spawning grounds (ANOVA: $F = 202.1$, df = 3, $P < 0.001$), and total percent lipid and water were precisely predicted based on BIA measurements ($R^2 = 0.82$, RMSE = 5.33; $R^2 = 0.78$, RMSE = 2.43 respectively). The BIA model was tested to determine if it could be generalized between similar species, but this was found to be less precise than species-specific models. The

BIA measurement technique was also easily implemented into an existing study on a remote Chinook Salmon population. Given threats from climate change and mining activities, this information will be useful for fisheries researchers as a benchmark for understanding migration behaviors in these Chinook Salmon populations, and indicates that integration of BIA into population monitoring may be a useful tool for creating management practices targeted at facilitating successful migration behaviors and increasing or maintaining energetic status for these fish.

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General Introduction

Pacific Salmon *Oncorhynchus* spp. undergo extensive migrations between their freshwater spawning and rearing habitats and abundant food resources in the ocean environment where they mature (Quinn 2005). As adults migrating up river to return to their spawning sites, they must have adapted certain behavioral (e.g., migration timing and rates) and physiological (e.g., energetic status) traits that will allow them to reach their spawning locations with enough time to deposit eggs that will develop into viable offspring. These offspring will then be able to migrate out to the ocean and survive to spawn years later, increasing their lifetime fitness. These adaptations, in part, are shaped by the difficulty of reaching the spawning location, which is influenced by the flow regime of the home river, the distance a fish must travel to its spawning location, and stream gradients encountered along the way (Crossin et al. 2004; Keefer et al. 2004).

In Alaska, Chinook Salmon *O. tshawytscha* is a species vital to the ecology, economy and culture of the state (Quinn 2005; Clark et al. 2006; Bottom et al. 2009). Recently, Chinook Salmon in Alaska have been in a period of low abundance, and many of the driving factors behind these declines remain unknown (ADF&G Chinook Salmon Research Team 2013). An understanding of how environmental and biological characteristics influence spawning distributions, migration patterns and energetic status may lead to insight into potential reasons for Chinook Salmon population declines and provide a benchmark for studying how these populations will respond to potential changes in their environment.

Migration Behaviors

Among salmon species, migrations of Chinook Salmon are the longest and most physiologically taxing. As the largest Pacific Salmon species, Chinook Salmon are able to swim

great distances and have been tracked to spawning locations as far as 3,000 km from the ocean into the Yukon River basin (Eiler et al. 2015). In Alaskan rivers, during April through August, mature Chinook Salmon return to their natal rivers, with peak runs typically occurring in June (Healey 1991). Once fish have reached their spawning locations, which range from small tributaries to large river mainstems, competition among individuals ensues for access to redd locations and reproduction partners (Quinn 2005). Relative to other, smaller bodied species, Chinook Salmon spawn in areas that have large cobble substrate and high flow velocities. Following competitive behavior for access to mates, females dig deep redds (up to 18 cm) in water up to 4 m deep (Healey 1991). The females then deposit eggs into these redds while males release sperm; the redd is then covered with substrate and will be guarded by the female for four to eighteen days until the spent salmon die (Healey 1991).

Migration timing and migration rates of Chinook Salmon have been shown to vary depending on the degree of difficulty of the spawning migration (Quinn 2005). Earlier returning fish may spend months in the river before reaching their final spawning locations, an adaptation that allows fish to populate areas of ideal spawning and rearing habitat that are far from the river mouth or pass through difficult barriers (Quinn et al. 2016). The river discharge regime may influence migration timing, as fish may take advantage of higher water levels to navigate river sections too shallow to pass during other times of the year (Quinn et al. 2016). Migration timing may also vary based on morphological characteristics such as sex, size and shape of fish. For example, often fish that have a sleeker body form tend to migrate farther to their spawning grounds relative to larger individuals, and may enter the river earlier (Roni and Quinn 1995; Crossin et al. 2004). Migration timing also differs between sexes; male salmon typically enter

rivers earlier than females to allow more time for competitive interactions and spawning site selection (Quinn 2005; Clark et al. 2015).

Migration rates, similar to migration timing, are also influenced by multiple environmental and biological factors in the river environment. A recent study conducted on Chinook Salmon migration rates found that fish that spawned farther upstream had faster migration rates than those that spawned in the lower river, and that fish slowed as they swam farther upriver (Eiler et al. 2015). Higher discharge rates in the river may also have an effect on migration rates, as studies have found that fish migration rates decreased in periods of high flow velocity, likely owing to the necessity to conserve energy to use in the remainder of their migration or due to fatigue from swimming against a current (Keefer et al. 2004; Hasler et al. 2012). An understanding of how physical and biological characteristics impact migration behaviors in adult Chinook Salmon can aid fisheries managers and researchers in understanding population dynamics (i.e. abundance estimates) and can be incorporated into more targeted management practices.

Energetic Status

Energetic status in Pacific Salmon is an important characteristic of the health of individual fish and strongly influences the ability of these fish to complete spawning migrations and successfully reproduce. Lipid stores make up the majority of energetic fuel for Pacific Salmon during upstream migrations (Brett 1995; Quinn 2005; Mesa and Magie 2006). Prior to spawning migration, it is important that individuals have stored enough lipid reserves to reach their spawning location, produce secondary sexual traits (e.g., dorsal hump in males), perform courtship behaviors, and produce viable gametes (Kinnison et al. 2003). As fish use these energy stores, they replace lipids with water to maintain their body shape (Hartman and Margraf 2008;

Stolarski et al. 2014). Protein is also used to provide energy for migrating salmon, though only after a majority of the lipid reserves have been depleted (Brett 1995). Fish that die on the way to their spawning locations (i.e., pre-spawning mortality) often do so owing to insufficient energy reserves and complications with man-made or environmental obstacles (e.g., dams and increased water temperature; Minke-Martin et al. 2017). Therefore, energetic status at river entry is an important factor to consider when monitoring stock health and can play a large role in migratory populations because lipid content is a critical factor to successful spawning.

Once the upstream migration is completed, salmon must have enough energetic stores remaining to complete their spawning activities (Brett 1995). Lipid content in spawning salmon varies by sex and spawning location distance due to differences in energetic requirements (Quinn 2005). Specifically, female salmon typically have a higher energetic demand owing to the need to produce energy rich eggs and thus require more lipid stores during spawning than males (Hearsey and Kinzinger 2015). Egg size and number in female salmon also differ based on spawning location distance, where individuals with more challenging migrations often have fewer and smaller eggs than those with shorter migrations (Kinnison et al. 2001). This indicates that the cost of migration is a major driver in the allocation of lipid stores, as fish with longer migrations divert more lipid stores to somatic tissues. While egg characteristics in females can change depending on the energetic cost of reaching spawning sites, males divert any lipid stores that are not used for swimming into secondary sexual characteristics and competitive interactions (Kinnison et al. 2003).

In previous studies, it has been shown that salmon will use almost all of their stored lipids in the spawning process, whether lipids are allocated towards migrations upstream or gamete development. For example, a study conducted on Sockeye Salmon *Oncorhynchus nerka* in the

Fraser River found that 60 to 86% of somatic lipids were expended by the end of spawning activities and fish with longer migration distances had higher lipid levels upon freshwater entry (Crossin et al. 2004). Similarly, a study on Chinook Salmon indicated that by the end of spawning, males used 99.6% of lipid stores and decreased protein levels by 30% in muscle tissues, whereas in visceral tissues they used 80.8% of lipid stores and decreased visceral protein levels by 16.3% (Mesa and Magie 2006). As Pacific Salmon are semelparous, energetic status during spawning activities is a major factor contributing to their ability to successfully reproduce in their lifetime.

In the past, quantification of energetic content to determine body condition in animals involved the lethal and time consuming method of proximate composition analysis or the use of condition indices such as Fulton's condition factor (K), relative weight (W_r ; Neumann et al. 2012) and analysis of residuals from species- or population-specific length-mass regressions (Bentley and Schindler 2013). These condition indices, though non-lethal, are not representative of energetic status as they cannot distinguish lipid from water weight (Sutton et al. 2000, Simpkins et al. 2003, Trudel et al. 2005).

Recently, methods have been developed to non-lethally and accurately estimate energetic status for fisheries studies (Cox and Hartman 2005). Bioelectrical impedance analysis (BIA) uses the properties of electrical conductivity (e.g., resistance and reactance) to predict indices of energy density such as total body lipids and water (Kyle et al. 2004). As lipids are nonconductive, resistance measurements are a measure of lipid content, whereas reactance is indicative of the volume of healthy cells in the body. Electrical metrics are then used to build species-specific models to predict energetic status via calibration with laboratory proximate composition analysis measurements (Cox and Hartman 2005; Cox and Heintz 2009; Stolarski et

al. 2014). In studies with an adequate sample size and total lipid range of a specific species, this method has been able to accurately predict energetic status for fishes (Hartman et al. 2015). Although there is some evidence that BIA predictive models are transferrable among closely related species (e.g., within families; Duncan 2008), the utility of predicting energetic status among large-bodied salmonid (Salmon and Trout) species, many of which are experiencing periods of low abundance or population declines, remains unknown. As such, the ability to non-lethally predict energetic status based on previously established models may be useful for conservation and monitoring of sensitive populations or species.

Objectives

In this study, I explored the effects of biological and physical factors on migration behaviors and variation in energetic status of Chinook Salmon in rivers in Alaska. First, migration timing and migration rate patterns in Chinook Salmon returning to two Southeast Alaska rivers were studied to understand basic characteristics of migration in these populations. The specific objectives for Chapter 1 were to 1) identify spawning locations of tagged individuals, 2) quantify migration timing, and 3) examine how migration rates vary in response to biotic and abiotic factors. The specific objectives for Chapter 2 were to 1) examine among-population differences in proximate composition (lipid, water, protein) of four Alaska Chinook Salmon populations, 2) build and evaluate predictive models based on the relationship between proximate components and BIA electrical measurements for the four populations, 3) assess the utility of among-species prediction of energetic status using Chinook Salmon and Chum Salmon *Oncorhynchus keta* BIA models, and 4) quantify relationships among BIA-predicted energetic status, sex, and spawning location for a remote Southeast Alaska Chinook Salmon population to investigate the feasibility of this method for monitoring energetic status. The results from these

studies will be useful for fisheries researchers as a benchmark for understanding migration behaviors in these Chinook Salmon populations, which will inform future studies that assess the responses of these populations to threats from climate change and mining activities. This study will also provide a new BIA model for Chinook Salmon and assess utility of this method in population monitoring that can allow for more targeted management practices focused on determining and maintaining energetic status levels that allow fish to survive to spawning.

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Chapter 1: Spawning migration behavior of Chinook Salmon *Oncorhynchus tshawytscha* in Southeast Alaska transboundary rivers[1]

ABSTRACT

Adult Chinook Salmon *Oncorhynchus tshawytscha* undertake extensive and energetically costly migrations between food resources in the ocean and their freshwater spawning habitats. As a result, migration behaviors such as river entry timing and swimming rates show local adaptations that that maximize reproductive success. Such adaptations may result from variable physical environmental drivers and may be manifested as individual- and population-specific biological characteristics. The transboundary Stikine and Taku Rivers (flowing from Canada into the United States) are two of the largest producers of Chinook Salmon in Southeast Alaska, which are an important resource for both United States and Canadian stakeholders, but relatively little is known about the migration characteristics of this species in these remote rivers. The overall goal of this research was to explore variation in migration timing and rates of Chinook Salmon in these rivers. Adult Chinook Salmon ($N = 673$) returning to the Stikine and Taku rivers were captured using drift gillnets and fish wheels during May–June 2015 and 2016, outfitted with uniquely coded radio tags, and subsequently tracked to spawning locations using basin-wide aerial telemetry surveys and stationary telemetry towers. Migration timing and rates were assessed as a function of biotic and abiotic factors using linear and mixed effects models. Mean migration timing was earlier for fish that spawned in farther upstream tributaries and in the Taku River compared to those in the Stikine River. Migration rates decreased during periods of high discharge and as fish moved farther upstream, were faster for fish with spawning sites further

[1] Neuneker, K.R., J.A. Falke, J.V. Nichols, A.C. Seitz, and P.J. Richards. Spawning migration behavior of Chinook Salmon *Oncorhynchus tshawytscha* in Southeast Alaska transboundary rivers. Formatted for *Transactions of the American Fisheries Society*.

upstream when compared to those that spawned lower in the river, and differed between river and study year. Given threats from mining activities and climate change, information about how physical and biological factors impact migration timing and rates will be useful for fisheries managers as a benchmark for understanding migration behaviors in Chinook Salmon populations.

INTRODUCTION

Migration behaviors are utilized by animals to move among habitats and capitalize on intermittently available resources where feeding or breeding opportunities may increase fitness (Dingle and Drake 2007). Birds, insects, and fishes all are well-known for their extensive migrations that increase these opportunities (Dingle 2006). These migrations may be movements that occur on an annual, seasonal, or life-long basis and are often energetically demanding and require unique physiological and behavioral adaptations (Bernatchez and Dodson 1987; Healey 1991; Crossin et al. 2004).

Adult Pacific Salmon *Oncorhynchus* spp. undergo extensive migrations between abundant food resources in the ocean environment and their freshwater spawning habitats (Brett 1995; Quinn 2005). During the freshwater migration phase, these fish do not feed and must rely on lipid stores, requiring them to adopt behavioral and physiological traits that will allow them to reach spawning locations at a time that maximizes survival of progeny (Minke-Martin et al. 2017). Such biological adaptations are shaped by temperature and flow regimes of the home river, as well as the degree of difficulty of the migration (e.g., distance to spawning sites and high gradient reaches or partial barriers passed; Crossin et al. 2004; Keefer et al. 2004; Keefer et al. 2015).

Among salmon species, migrations of Chinook Salmon *O. tshawytscha* are among the longest and most physiologically arduous (Healey 1991; Quinn 2005). For example, some populations of this species have been tracked to spawning locations in the Yukon River basin located as far as 3,000 km from the ocean (Eiler et al. 2015). In Alaska, most Chinook Salmon spend their first year of life in the riverine environment (i.e., stream-type life history) before outmigrating to the ocean, where they remain for one to five years feeding throughout the northern Pacific Ocean (Healey 1991). During April through August, Chinook Salmon in Alaska return to their natal rivers, with peak runs typically occurring in June.

Migration behaviors in adult Chinook Salmon have been found to be influenced by multiple environmental and biological factors (Quinn 2005). For example, river discharge and associated variation in flow velocity over space and time impacts fish swimming rates, and can directly affect the ability of fish to reach their spawning habitats (Keefer et al. 2004). Generally, increasing river discharge is correlated with reduced migration rates, and extreme flow can create obstacles where the flow velocity is too fast for fish passage. Earlier returning fish may spend months in the river before reaching their final spawning locations, an adaptation that allows fish to pass through difficult barriers or populate areas that are far from the river mouth (Jepson et al. 2010; Quinn et al. 2016). Often, fish that spawn farther up rivers have earlier river entrance dates and swim at faster rates to reach their spawning river (Clark et al. 2015; Eiler et al. 2015). Individuals may respond to high flow or longer migration distances by adjusting their behavior in freshwater, such as swimming slower or faster to avoid difficult conditions (Keefer et al. 2004). The relationship between migration characteristics and physical drives is important to understand because in the future, environmental characteristics are predicted to change during the Chinook

Salmon spawning migration period owing to climate change, and may impact migration behaviors (van Vliet et al. 2013; Shanley and Albert 2014; Kovach et al. 2015; Sloat et al. 2016).

Chinook Salmon migration behaviors have been shown to vary with biological characteristics such as body size and sex. For example, in some populations, individuals that have a sleeker body form tend to migrate farther to their spawning grounds relative to larger individuals, and males typically enter rivers earlier than females to allow for more time to compete for access to females (Roni and Quinn 1995; Crossin et al. 2004; Clark et al. 2015). Recent work has suggested that population declines in Alaska may be, in part, influenced by decreases in Chinook Salmon body size which has led to the return of smaller, less fecund individuals (Lewis et al. 2015). An understanding of the relationship between biological characteristics and migration traits may inform efforts to understand population dynamics of this species.

Chinook Salmon provide important ecological resources for marine and terrestrial animals, are essential to the livelihood of commercial, sport and subsistence fishers, and are regarded as a cultural icon by many user groups (Quinn 2005; Clark et al. 2006; Bottom et al. 2009). Recently in Alaska, Chinook Salmon have been returning to river systems in low numbers, putting many of the ecological, economic, and cultural benefits of this species at risk (ADF&G 2013). Of particular interest are the Stikine and Taku Rivers, two transboundary rivers (flowing from Canada into the United States) that are major producers of Chinook Salmon for British Columbia and the Southeast Alaska region. These rivers provide fisheries resources for Alaskans, Canadians and the Tahltan and Tlinigit First Nation groups in Canada, and annually account for > 80% of the wild Chinook salmon production in the region.

Migratory patterns and behaviors in remote populations of Chinook Salmon, such as those in the Taku and Stikine Rivers, are poorly understood, but important to study for a variety of applications, including adaptive management strategies and a better understanding of abundance and population dynamics. Studies of migration behaviors can provide information on spawning locations, overall abundance, regional abundance, and the exposure of fish to in-river fisheries (Eiler et al. 2015; Richards et al. 2015a, 2015b). Ultimately, migration information may lead to a better understanding of the attributes that make successful spawners, and help fisheries managers understand potential reasons why many salmon populations are currently in decline.

Although migration characteristics for Chinook Salmon have recently been studied in much larger (e.g., Yukon River basin; Eiler et al. 2014, 2015), and smaller systems in Alaska (e.g., Togiak River; Clark et al. 2015), little is known of their migration characteristics in the heterogeneous, glacially-influenced, transboundary rivers of Southeast Alaska. With recent population declines observed throughout the state and mining activities occurring in the Stikine and Taku drainages (e.g., Red Chris Mine and Tulsequah Chief Mine), it is important to understand the basic characteristics of migration and distribution of spawning populations in adult Chinook Salmon.

The overall goal of this research was to quantify variation in migration timing and rates of Chinook Salmon in two transboundary Southeast Alaska rivers. Over two years, we used radio telemetry to 1) identify spawning locations for tagged individuals, 2) quantify migration timing, and 3) quantify migration rates. We examined the influence of physical and biological factors such as river discharge, spawning location distance, sex, and body length on variation in migration timing and rates between rivers and years.

METHODS

Study area.—This study was conducted in the Stikine and Taku River basins in Southeast Alaska. The Stikine River is the largest transboundary river basin (51,593 km^2 watershed area; mean annual discharge = 1,580 m^3/s) and second largest Chinook Salmon producer in Southeast Alaska (Figure 1.1). Originating in north-central British Columbia, the river flows approximately 650 km westward to its mouth near Wrangell, Alaska. Generally, the Stikine River is characterized by numerous clear, rain-, snow-, and groundwater-fed tributaries that flow into a glacially turbid primary channel. Chinook Salmon spawning is limited to the lower half of the drainage (15,337 km^2) by a large, narrow canyon near the confluence of the Tuya River which impedes the migration of anadromous salmon (ADF&G 2013). Mean escapement (i.e., the number of salmon that have returned to their spawning streams and have escaped fisheries) for large (≥ 660 mm mid eye to fork length [MEF]) Stikine River Chinook Salmon between 1975 and 2016 was 25,000 individuals, ranging from 5,723 fish in 1976 to 63,523 fish in 2001, with approximately 50% of spawning occurring in the Tahltan River (Jaecks et al. 2013). Following the 2001 high, the number of fish returning to the river declined with an estimated 10,344 spawners returning in 2016 (Alaska Department of Fish and Game unpublished data). The biological escapement goal determined by the Alaska Department of Fish and Game (ADF&G; i.e., the number of fish deemed necessary by managers that must return to their spawning rivers to maintain a sustainable population) for this river ranges from 14,000 to 28,000 fish (Munro and Volk 2016). Other major spawning locations include the Verett, Iskut, and Chutine Rivers, as well as Andrew and Christina Creeks (Richards et al. 2015b). Chinook Salmon typically return to the river between early May and mid-July.

The Taku River is the largest Chinook Salmon producer (mean escapement = 36,000 fish) and second largest transboundary river basin (17,094 km^2; mean annual discharge = 387 m^3/s) in Southeast Alaska (Figure 1.1). This river has a biological escapement goal between 19,000 and 36,000 large Chinook Salmon, with a maximum escapement of 114,938 in 1997, and a minimum of 9,794 fish in 1983 (Munro and Volk 2016). Similar to the Stikine River, the Taku River has recently experienced population declines, with only 12,381 fish estimated to have returned to the river in 2016 (Alaska Department of Fish and Game unpublished data). The river originates in northwest British Columbia and flows southwest to Taku Inlet near Juneau, Alaska. Similar to the Stikine River, the Taku River is a glacially fed system, with many clear water tributaries. While the majority of spawning is thought to occur in the upper Nakina River, other major spawning locations include the Taku River mainstem, and the Nahlin, Dudidontu, Kowatua and Tatsatua Rivers (Richards et al. 2015b). Fish typically return to, and are sampled in, the Taku River from the end of April to mid-July.

Fish capture and radiotagging.— Adult Chinook Salmon were captured in the lower reaches of each river, near the sampling sites of ADF&G ongoing annual mark - recapture studies (Richards et al. 2015a, 2015b). Specifically, tagging of fish on the Stikine River took place near Kakwan Point (56° 41'41.75" N, 132° 13'20.47" W) and Taku River fish capture and tagging occurred in the vicinity of Canyon Island (58° 32'55.59" N, 133° 40'50.20" W). All sampling occurred during May–July of 2015 and 2016.

Fish were captured using drift gillnets (18.4-cm stretch mesh, 36.6-m long x 5.5-m deep) and fish wheels (Taku River only), at the aforementioned sampling sites (Richards et al. 2015a, 2015b). Upon capture of large, adult Chinook Salmon (≥ 660 mm MEF) as indicated by a bobbing motion of gillnet corks or release from a fish wheel holding box, fish were placed into a

neoprene cradle and immersed in a live well containing fresh river water. Only fish above this size threshold were outfitted with radio tags so that tag size would not exceed 2% of fish body weight, and to ensure that the study focused on fish that had spent at least three years in the ocean (Liedtke and Rub 2012; Jaecks et al. 2015). These fish also correspond to those of a legal harvestable size that are used to estimate escapement and determine if escapement goals are reached. Fish deemed to be healthy (e.g., no bleeding injuries, loss of color or equilibrium), were then measured (MEF), classified to sex based on morphology, and radio tagged. Advanced Telemetry Systems (ATS, Isanti, Minnesota) F1845B radio tags weighing 26 g, 52-mm length (19-mm diameter) with a 30-cm antenna, and a 180-day battery life were used to track Chinook Salmon. Tags operated on frequencies that ranged from 150.000–152.999 MHz. Each tag had a unique frequency and code combination to identify individual fish and a mortality signal was triggered if the tag was inactive for a period of 24 hours (Richards et al. 2015a, 2015b). Esophageal radio tags were carefully inserted through the mouth to the stomach, using a 1-cm diameter, 30-cm long plastic pipe. After tagging, individual fish were inspected to ensure that the radio tag was secured (antenna protruding from the esophagus) and immediately released.

Fish tracking.— Radio tagged Chinook Salmon were tracked using a combination of remote receiver stations and aerial surveys. Remote tracking stations were erected at stable locations along the riverbank (Figure 1.1). These points were selected to document fish passage past important locations such as spawning tributaries, the United States – Canada border, boundaries of Canadian commercial fisheries, and a landslide location associated with the Tahltan River within the Stikine River drainage. Tracking towers were composed of ATS 4500 C receiver data logger systems, powered by 12-volt batteries and solar panels (Eiler et al. 2015). Each tower had two-directional Yagi antennas aimed downstream and upstream of the station.

Remote receivers continuously scanned through preprogrammed frequencies (150.000-152.999 MHz) to search for any transmitting tags in the vicinity of the station. Upon detecting a tag, the receiver recorded the transmitter's frequency, code, signal strength, mortality status, the day of year, and time of day at 10 minute intervals (Richards et al. 2015a, 2015b). In addition to remote stations, basin wide aerial surveys were conducted approximately every two weeks throughout the spawning period (July to September) on both rivers. During aerial tracking, fixed-wing or helicopter aircraft were outfitted with two externally mounted antennas and two 4520C ATS datalogger receivers. Detections were recorded while the aircraft was flying at approximately 300 m above each river's surface. Data loggers during aerial surveys recorded GPS coordinate information along with the transmitter's frequency, code, day of year, time and mortality indicator (Richards et al. 2015a, 2015b). Tag locations, time of detection, signal strength and mortality indicators from tracking tower data and aerial surveys were uploaded into a geographic information system (GIS) using ArcGIS software version 10.2.1 (Environmental Systems Research Institute, Redlands, California).

Fish locations and movement rates.— Migration timing was defined as the day of year that an individual was captured and tagged, which corresponded with the first documented day in the river. Final locations for individuals were defined as the farthest upstream location given that the fish displayed progressive upstream movements through all detections or if subsequent downstream movements were less than 5 km from the furthest upstream location. While a majority of the final locations for individual fish was their farthest upstream location, of the few that were not, the location with the highest signal strength for which reasonable evidence of milling behavior (multiple detections) existed was assigned as the final location (Yanusz et al. 2013; Eiler et al. 2015). Fish that were deemed to have stayed in the river system in which they

were tagged and entered a spawning tributary were assumed to have spawned at these final locations. Although some fish have been observed spawning in the Taku River mainstem, tags with a final location in the mainstem were excluded from analysis, as many of these fish were harvested, had died, or may have still been travelling to their final location (Keefer et al. 2004). Tag detection range resolution has been shown to be approximately 1.6 km, and we assumed fish positions were within this range (Burger et al. 1985; Eiler 2012). Distance (km) from the river mouth to final fish locations (hereafter spawning location distance) was measured in ArcGIS based on HydroSHEDS stream polylines for the Stikine and Taku Rivers (Lehner et al. 2008).

Movement rates of fish were determined using stationary tower data to ensure that rates were comparable and captured the progressive upstream movements of fish (Eiler et al. 2015). Movement rates (km/d) were calculated by measuring the minimum fish travel distance (i.e., stream distance (km) between tower locations), divided by the time difference between subsequent detections (d). Specifically, these rates were calculated using the time of final detection at each tower, and only fish that had constant upstream movement and sequential tower detections were used for analysis (Heim et al. 2016). Distance between towers (reach distance; km) was measured using ArcMap, under the assumption that fish travelled along the thalweg of the river between detection periods (Eiler et al. 2015). River reaches were defined as the distance between two towers (i.e. reach 1 = tower 1 – tower 2; Figure 1.1).

Statistical analysis.—Migration timing (response variable) was modeled as a function of sex (male or female; factor), length (mm; continuous variable), distance to spawning location (km; continuous variable), river discharge (m^3/s; continuous variable), river (Stikine or Taku; factor) and year (2015 or 2016; factor) using a generalized linear model. River discharge was obtained from stream gauge sites near tagging locations on the Stikine (15024800) and Taku

(15041200) Rivers (http://waterdata.usgs.gov), as a three-day average that included discharge values on the tagging date and days prior to, and following, tagging. Variables were tested for multicollinearity using the variance inflation factor (VIF), and were removed if the VIF was > 10. An information theoretic approach was used to select the best model that described migration timing, given the data (Burnham and Anderson 2002). Akaike's information criteria (AIC), was used to evaluate a set of candidate models that included 1) a global model containing all predictors ($N = 1$), 2) single variable models ($N = 6$), 3) models containing all covariates but one ($N = 5$) and 4) models including only physical parameters (discharge, river and year, $N = 1$) or 5) biological parameters (sex and length, $N = 1$), for a total of 14 candidate models. Spawning location distance was included in all models. The model with the smallest AIC value and the highest AIC weight (w_i) was selected as the top model. To account for model uncertainty, we used model averaging to calculate parameter estimates and unconditional confidence intervals for the confidence set of models with Akaike weights (w_i) > 0.05. Models were constructed in Program R (R Development Core Team 2012) and analysis was done using the Multi-Model Inference package *MuMIn* (Bartoń 2015).

We used a mixed-effects model to examine relationships among environmental and biological factors and upstream movement rates of tagged Chinook Salmon in the Stikine and Taku Rivers (Zuur et al. 2009). Migration rate (km/d; response variable) was modeled as a function of fixed effects that included sex, length, spawning (distance from river mouth to spawning location; km), day of year tagged, discharge (averaged between day of detection at each tower), upstream distance at detection (distance of each tower location upstream; km), river, and year. The identity of individual tagged fish (transmitter ID) was included as a random effect in all models to eliminate effects of pseudoreplication. Candidate models were constructed

similarly to migration timing models, where year and river covariates were included in all models for a total of 19 candidate models. Model selection and averaging for migration rate analysis were conducted in the same manner as described above. All statistical analyses were conducted using Program R ver. 3.4.1 (R Development Core Team 2012), and we used the *MuMIn* package (Bartoń 2015) for model averaging.

RESULTS

A total of 1,021 adult Chinook Salmon ≥ 600 mm MEF were captured and tagged on the Taku and Stikine Rivers in 2015 and 2016 (Table 1.1), of which 673 were tracked to a spawning location. Of these 673 fish, 434 were female and 239 were male and lengths of tagged fish ranged from 660 to 980 mm (mean =760.1 mm, SD = 58.1). In the Stikine River, 176 and 94 fish were tagged and tracked in 2015 and 2016 respectively, and in the Taku River, 253 and 150 were tagged and used for analyses in 2015 and 2016. Mean tagging date in both rivers was June 4th (mean = 155.3 day of year, SD = 13.7; Stikine River mean = 160.1 day of year, SD = 14.6; Taku River mean = 152.2 day of year, SD = 12.0). In the Taku River basin, the Nakina River tributary had the highest proportion of tagged individuals with 46% (N = 189), while in the Stikine River, the Tahltan River tributary had highest proportion of tagged fish (48%; N = 131).

Migration Timing

Overall, fish that entered into a river earlier spawned at more distant locations (Figure 1.2), and Taku River fish entered approximately eight days earlier than fish from the Stikine River (Figure 1.3). In the Stikine River, fish from the spawning tributary closest to the river mouth (Andrew Creek) had an earlier migration timing (mean = 181.7 day of year, SD = 7.0) than fish that spawned in the tributary farthest from the river mouth (Tahltan River; mean = 159.7 day of year, SD = 13.0). In the Taku River basin, fish that spawned in the tributary closest

to the river mouth (King Salmon River) had earlier migration timing (mean = 148.0 day of year, SD = 15.6), than those that spawned in the tributary farthest from the river mouth (Nahlin River; mean = 150.2 day of year, SD = 14.0; Figure 1.4). The highest ranked model for migration timing represented 20% of the weight of candidate models ($w_i = 0.20$; Table 1.2) and indicated that Chinook Salmon migration timing was earlier for fish that spawned at more distant sites, and varied by river. Six other models appeared in the confidence model set ($w_i > 0.05$), and model-averaged estimates further suggested that migration timing differed among years, with 2015 migration occurring earlier than 2016, and earlier migration timing with lower discharges, and for smaller fish. However, unconditional 90% confidence intervals for all covariates except distance and year overlapped zero, indicating considerable uncertainty in these estimates.

Migration Rate

Migration rates varied among individual Chinook Salmon and tributary groups. The migration rate for all migrating Chinook Salmon ranged from 0.07 to 80.35 km/d (mean = 13.29 km/d, SD = 12.51). For both rivers combined, reach 1 (tower 1 – tower 2) had the highest mean migration rate (mean = 18.09 km/d, SD = 10.25) and reach 6 (tower 6 – tower 7) had the lowest mean rate (mean = 1.76 km/d, SD = 1.03). In the Stikine River, reach 1 rates ranged from 0.47 to 50.56 km/d (mean = 24.13 km/d, SD = 13.55), whereas Taku River fish reach 1 migration rates were between 0.28 and 44.77 km/d (mean = 15.59 km/d, SD = 7.22; Figure 1.9; 1.10). Farthest upstream reach rates for fish from the Stikine River basin ranged from 0.07 to 25.92 km/d (mean = 1.76 km/d, SD = 1.02), whereas Taku River basin final reach migration rates for fish were from 0.35 to 80.35 km/d (mean = 6.63 km/d, SD = 7.31). Within the Stikine River basin, fish migrating to the Verett River (110 rkm), had the lowest mean migration rates (mean = 12.55 km/d, SD = 16.79), whereas fish migrating to Christina Creek (121 rkm), had the highest rates

(mean = 18.09 km/d, SD = 15.04). In the Taku River basin, Sloko River (117 rkm) migrants had the lowest mean migration rates (mean = 8.98 km/d, SD = 5.97), whereas those from the Dudidontu River (207 rkm) had the highest rates (mean = 13.93 km/d, SD = 14.98).

The top mixed-effects model indicated that year, river, discharge, spawning location distance, sex, and upstream distance had the largest effect on migration rates of Chinook Salmon from the Stikine and Taku Rivers (w_i = 0.45, Table 4). Seven models were included in the confidence model set, with sex, length, and date tagged covariates having unconditional 90% confidence intervals that overlapped zero (Table 1.5). Model-averaged estimates indicated that tagged fish swam at a slower rate in 2016 relative to 2015, and fish in the Taku River swam slower than Stikine River fish (Figure 5). Also, as discharge increased, migration rates decreased and as fish moved further upstream, their migration rate slowed (Figure 6; Figure 7). Migration rates were also higher for fish that spawned at sites farther from the river mouth.

DISCUSSION

Chinook Salmon populations spawning in Alaska transboundary rivers provide important resources for Alaskan and Canadian user groups, and currently face threats to their spawning habitat from environmental changes due to climate change and mineral exploration and development (Richards et al. 2015a, 2015b). Our assessment of Chinook Salmon migration rates and timing in remote Alaskan rivers provide important information for conservation and management of this species in two southeast Alaska transboundary systems. This study found that the migration traits of Chinook Salmon in these river systems were influenced by environmental characteristics of their river habitat. Knowledge of movement patterns and how these behaviors are influenced by environmental characteristics can be useful for managers to

better understand population specific impacts of fisheries and changes in environmental conditions (Eiler et al. 2015).

Migration Timing

In this study, migration timing (tagging date) was most strongly influenced by distance to spawning grounds. The finding that fish destined for distant spawning locations entered the river earlier in the season could be an adaptation to the increased time required to reach their spawning grounds, as fish that spawn farther upstream have increased residency within the river (Eiler et al. 2014). Similar to the results from this study, previous research on Pacific salmon has shown earlier river entry dates with increasing distance to spawning locations (Burger et al. 1985; Clark et al. 2015). Within this overarching pattern of earlier entry for more distant spawning locations, there was some variability in the migration timing of different tributary groups in both the Stikine and Taku Rivers. This was likely the result of the diverse spawning habitats available to fish in these rivers. Tributaries of the Stikine and Taku river basins represent a heterogeneous set of geomorphic and hydrologic conditions comprised of glacial-, rain-, or snowmelt-dominated flow regimes. As a result, temperature regimes in these tributaries vary widely, resulting in variation in development rates of offspring, and ultimately in variability in run timing among the tributary stocks (McPherson et al. 1996; Crossin et al. 2004; Quinn 2005; Richards et al. 2012; Lisi et al. 2013; Quinn et al. 2016). However, high elevation, steep gradients, and cold water temperatures typically are confounded with distance from a river's mouth (i.e. sites farther upstream from the river mouth are more likely to be higher in elevation) making it difficult to tease apart processes influencing migration timing behavior. Regardless, the pattern of earlier migration timing for individuals that spawned at distant locations was strong and consistent between the two rivers.

Differences in mean migration timing between drainages were evident in this study, in which Taku River fish had earlier mean migration dates than those in the Stikine River. In the Taku River, fish spawn at numerous locations throughout the basin, creating early, middle and late runs (Parken et al. 2006). The earlier migration timing for Chinook Salmon returning to the Taku River compared to the Stikine River could be due to the higher incidence of spawning locations in the Taku River located farther from the river mouth. For example there are eight spawning tributaries that were located farther than 120 km (i.e., roughly half the farthest mean spawning location distance between both rivers, at 245 km) upstream in the Taku River compared to two spawning locations farther than 120 km upstream in the Stikine River. The presence of more distant spawning locations may require fish to spend more time migrating, and therefore they may enter earlier into the river (Keefer and Caudill 2014). The inaccessibility of upstream spawning habitat in the Stikine River basin may result in only middle or late runs being the dominant migration timing strategy (E. Jones, Fishery Biologist, Alaska Department of Fish and Game, personal communication). Thus, inter-basin differences between accessible area and the amount of potential spawning habitat may contribute to the observed earlier mean migration timing for the Taku River, where more spawning locations farther upstream in the Taku River make the mean migration timing earlier in this river system.

The difference in migration timing between the Stikine and Taku Rivers is likely not affected by the proximity of entry locations for Chinook Salmon returning from their outside rearing waters in the Gulf of Alaska to the river mouths (ADF&G 2013). There are two major points of entry for Chinook Salmon returning to the Stikine and Taku Rivers, Icy Strait in the north and Chatham Strait to the south, and individuals that return through Icy Strait are likely to reach the mouth of the Taku River prior to the Stikine River mouth (Orsi et al. 2013).

Information from coded wire tags show that salmon return to southeast Alaska from both entry points, indicating that the location from which fish return to southeast Alaska from these outside rearing habitats may not play a large role in migration timing into the river system (Alaska Department of Fish and Game Mark, Tag and Age Lab 2017). Once fish enter the inside waters of Southeast Alaska from the major entry points at Icy and Chatham Straits, they may have different swimming patterns that result in the Taku River fish reaching the river mouth earlier, but little is known about these marine migrations.

Migration Rate

River discharge, spawning distance, and distance upstream affected upriver migration rates of Chinook Salmon in the Stikine and Taku Rivers. Our results agreed with those of other salmon migration rate research (Keefer et al. 2004; Hasler et al. 2012; Strange 2012) that demonstrated Chinook Salmon migration rates decreased with increasing discharge, and increased with increasing spawning location distance. Salmon have an optimal swimming speed of one body length per second that is often utilized when migrating long distances to minimize the cost of transport. This optimal speed is particularly important to consider when salmon are migrating upstream to spawn as they have a fixed energy budget (Bernatchez and Dodson 1987). Decreasing migration rates as a response to increasing discharge is likely due to fish avoiding expending too much energy in areas with periodic high flow velocities. It may also be due to fish resting after attempts to swim through locations with consistently high flow velocities, which may cause fatigue (Bernatchez and Dodson 1987). The reduced speed for fish as they swam farther upstream may be attributable to increasingly depleted energy resources and the need to conserve energy for spawning. Fish may also have slowed in order to have more time to

correctly identify chemical cues and successfully home to their natal stream (Keefer and Caudill 2014).

Chinook Salmon migration rates on both the Taku and Stikine Rivers were slower in 2016 than in 2015 and Taku River fish migrated slower than those in the Stikine River. Migration rates may have been slower in 2016 due to natural variability between years, as the rates in 2016 were only slightly lower than those observed in 2015. Data from more years may be necessary to determine if the slower rates in 2016 were due to natural variability or other factors, as other studies that have three or more years of migration pattern data have found that these migration rates and timing remain relatively consistent across years (Keefer et al. 2004; Eiler et al. 2014, 2015). Taku River fish may have slower migration rates than Chinook Salmon from the Stikine River due to the earlier migration timing of Taku River fish, where they may not need to swim as fast to reach their spawning locations. There are also more fish spawning in the lower portion of the Taku River, as 51% of fish spawned lower than 120 km from the mouth in the Taku, while 35% of fish spawned below this same distance threshold in the Stikine River. Fish that migrate farther upstream tend to swim faster throughout their migration than those that spawn in more downstream locations, this may cause the mean migration rates for fish in the Taku River to be lower.

Although much smaller in basin area than other Chinook Salmon bearing river basins such as the Yukon and Columbia Rivers, Stikine and Taku River fish behaved similarly with respect to migration rates. For example, similar to this study, Eiler et al. (2014, 2015) showed that Chinook Salmon in the Yukon River basin migrated faster if destined for farther spawning locations, and different migratory patterns and strategies existed among tributary stocks. Also, Chinook Salmon in the Columbia River were found to have slower migration rates at times of

higher discharge (Keefer et al. 2004), similar to our observations in Southeast Alaska. In the Togiak River in western Alaska, similarly sized to the Stikine and Taku Rivers, Chinook Salmon spawning in more distant tributaries entered the river, on average, earlier compared to lower river stocks (Clark et al. 2015). Taken in combination with our results, similar findings from the Columbia, Yukon and Togiak Rivers offer evidence that Chinook Salmon migration behaviors are similar across river basins, regardless of size or geographic location.

Biological Factors

We found no evidence for variation in Chinook Salmon migration timing or migration rates between males and females, or as a function of body length. In contrast, previous studies on migrating adult Pacific Salmon have documented that male salmon typically migrate into freshwater earlier relative to females to allow increased opportunities for competitive interactions (Quinn 2005; Clark et al. 2015). Additionally, in some studies, smaller bodied individuals have been shown to spawn in more distant tributaries, have earlier migration times, and faster migration rates (Roni and Quinn 1995; Crossin et al. 2004; Quinn et al. 2016). An explanation for the lack of relationship between migration behavior and body size in this study could have been the large size (e.g., > 660 mm MEF) of tagged individuals. We also found no relationship between migration behavior and sex. Tagging of larger individuals could have led to the study being biased towards females, as males (64% female and 36% male tagged individuals, and female to male ratio of roughly 2:1) were often smaller than females (i.e., jacks) and thus were not tagged. If sex bias was important it would be more difficult to discern patterns in migratory behavior between males and females. Tagging a wider size range of fish, particularly Chinook Salmon < 660 mm MEF, which comprised 40% of the catches, could lead to more insight toward differences between migration patterns of smaller and larger fish, as well as

between sexes. However, these results may also suggest that environmental factors have a more influential effect on the migration behaviors of Chinook Salmon in these two Southeast Alaska rivers. The Stikine and Taku Rivers are both relatively short systems compared to other basins where Chinook Salmon migration patterns have been studied, such as the Yukon or Columbia Rivers, and differences between sexes and the influence of size may have relatively little influence on migration characteristics of fish from these southeast Alaska populations.

Distance to spawning location was an important influence on both migration timing and migration rates of Chinook Salmon in the Stikine and Taku Rivers. This implies that the spawning locations for these fish are very important drivers of migration behaviors, and could indicate strong genetically-controlled local adaptations related to migration behavior. Previous genetic population classifications have found Chinook Salmon populations within and between the Stikine and Taku Rivers to be genetically similar, though these relationships are not fine scale and more research is being done to further tease apart the genetic relationship among stocks (Guthrie and Wilmot 2004; Seeb et al. 2007; Templin et al. 2011). Regardless, maintaining genetic heterogeneity among these populations is important for their persistence, and something managers should consider when developing escapement-based management plans focused on allowing enough fish from different spawning tributary populations to reach their spawning grounds (Schindler et al. 2010).

Assumptions

Additional factors that could have influenced the results of this study are related to assumptions of the tagging process (Richards et al. 2015a, 2015b). The first assumption was that the cumulative distribution of tagged fish through time would be similar to the cumulative distribution of fish returning to the river over the same time period. To meet this assumption tags

were distributed across weeks in proportion to the number of individuals caught to spread out the 300 available tags over the tagging period (May-July) dedicated to each river system. We also assumed that the tag did not have a behavioral effect on fish. Although radiotagging studies have shown Chinook Salmon to display delayed upstream migration after being tagged with externally mounted radio transmitters (Bernard et al. 1999), other studies using esophageal tags have found little evidence for negative behavioral impacts on salmon migration behaviors (Burger et al. 1985; Keefer et al. 2005; Eiler et al. 2014; Clark et al. 2015). In our study, most individuals (67%) continued upriver and were successfully tracked to their spawning locations suggesting that tagging did not considerably alter behavior. The last assumption was that final locations of fish were actual spawning locations used by Stikine and Taku river Chinook Salmon. We used a conservative weight of evidence approach to determine final locations, therefore we believe this rigorous process resulted in accurate spawning location determinations.

Implications

Benchmark migration characteristics information, such as that described in this study, will be critical for monitoring biological and ecological changes in Chinook Salmon populations from the Stikine and Taku Rivers into the future. Potential threats from mining activities and associated habitat alterations or water quality changes exist in Southeast Alaska rivers (Ream and Merriam 2017), and migrating salmon can be especially vulnerable to these changes (Quinn 2005). Acid mine drainage and an influx of metals into the environment can negatively impact salmon through releasing sediment into the river environment, obstructing gill tissue and inhibiting their ability to breathe, or through deadening olfactory senses upon which they rely for homing behaviors and predatory alarm cues (Saunders and Sprague 1967; Baldwin et al. 2003; McIntyre et al. 2012; Keefer and Caudill 2014). Mines in the upper basin of the Stikine and Taku

Rivers, if not correctly regulated, could be harmful to these salmon stocks and the wildlife and people that rely on them as a resource. Mining activities occurring in these Canadian headwater areas are one of the prominent management issues that will need to be addressed by both US and Canadian agencies, with the knowledge that maintaining high quality spawning habitats for these stocks is critical to healthy populations and sustainable fisheries. The ability of managers and researchers to monitor changes in behavior based upon deviation from benchmark estimates presented in this study, as well as the knowledge of how the environment affects fish will be important for better understanding how mining activities and effects from climate change may impact Chinook Salmon in these transboundary rivers.

This study provides evidence that migration behaviors of adult Chinook Salmon are influenced by the physical characteristics of their environment. Considering the projected changes in river discharge and temperature due to climate change, or changes in water quality and habitat from mining activities, the results from this study may be an important consideration for fisheries managers (Eiler et al. 2015; Richards et al. 2015a, 2015b). For example, climate change is projected to increase river temperatures and flows, and based on this research, one would expect to see either decreased migration rates or earlier migration timing, potentially causing increased prespawning mortality from higher energy expenditure, missed spawning opportunities, or reduced fecundity and lower egg quality (Shanley and Albert 2014). Additionally, there is potential for a mismatch between migration timing and discharge patterns where fish may encounter higher flows than those to which they have become adapted. The 33% of fish that were not tracked to spawning locations are also a concern for management agencies when trying to meet and maintain escapement goals for these rivers. These fish with unknown spawning locations either died en route, were harvested, or were still located in the mainstem at

their final location and thus not categorized into a spawning tributary. However, Chinook Salmon have been shown to be highly adaptable to changing environmental conditions in Southeast Alaska and have already displayed shifts in migration patterns to compensate for changes in river habitat (Kovach et al. 2015). Regardless, future research should focus on monitoring migration behaviors across the region, assessing how environmental and biological characteristics influence these behaviors and understanding how these environmental factors and behaviors may be affected by habitat alterations due to climate change and human impacts.

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FIGURES AND TABLES

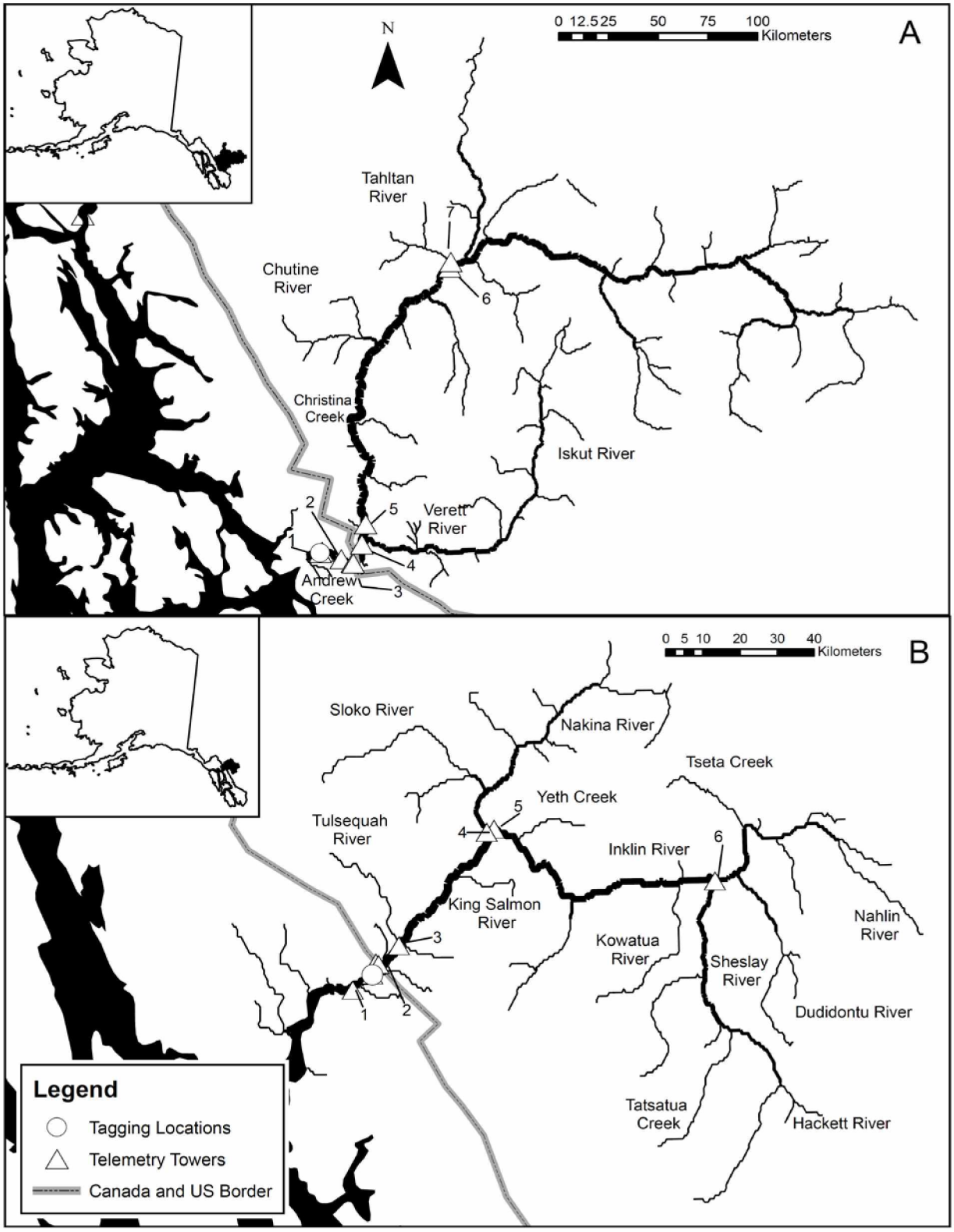

Figure 1. 1. Stikine (A) and Taku (B) Rivers study areas in Southeast Alaska (insets). Locations of stationary towers (triangles), radiotagging sites (circles), and major Chinook Salmon spawning tributaries are shown. Towers are identified by numbers, stream reaches are areas between towers. On the Stikine River reach 1 = 12.95, reach 2 = 12.02, reach 3 = 6.89, reach 4 = 14.97, reach 5 = 175.71, reach 6 = 3.65 rkm. On the Taku River reach 1 = 10.04, reach 2 = 7.74, reach 3 = 50.01, reach 4 = 2.45 rkm.

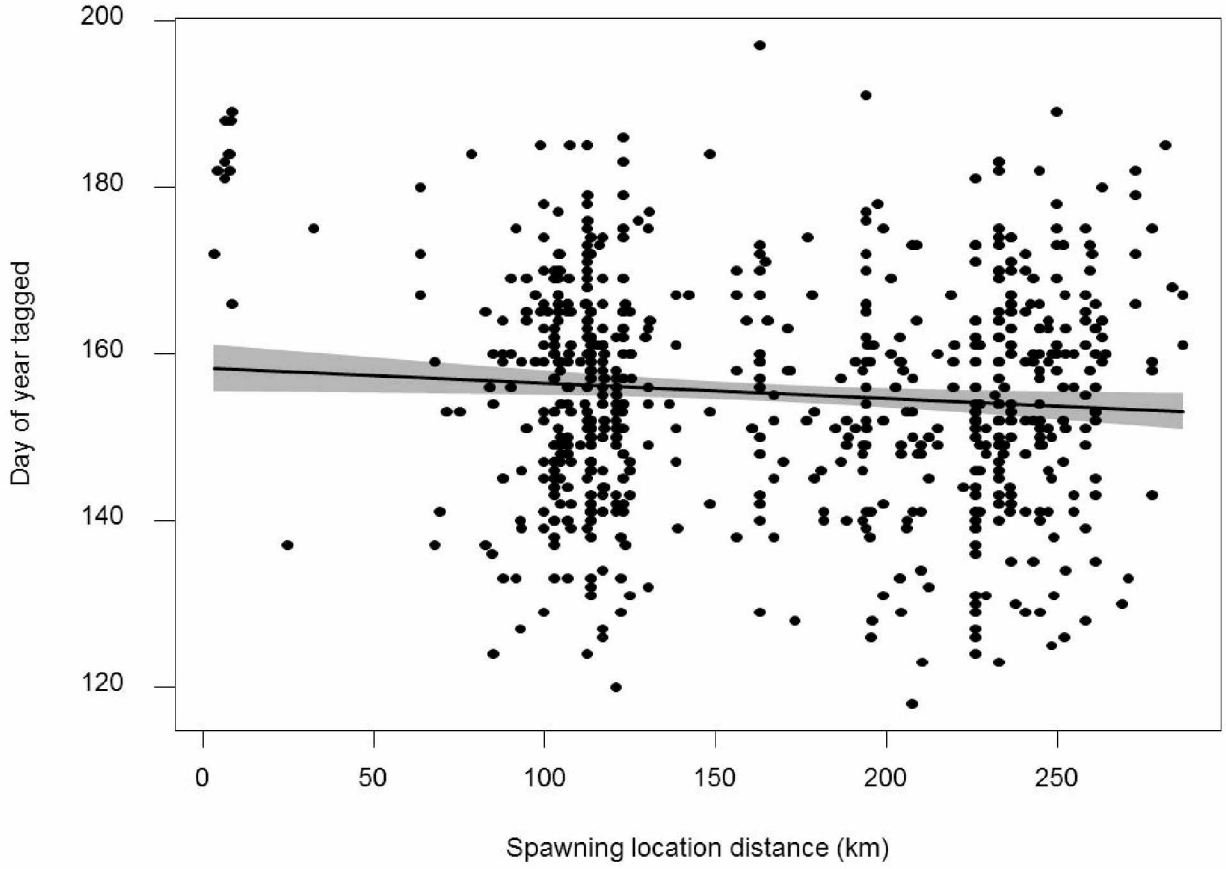

Figure 1. 2. Relationship between tagging date (day of year after 1 January) of Chinook Salmon in the Stikine and Taku Rivers and distance to spawning locations. The line (± 95% confidence interval band) is the estimated relationship from a generalized linear model (Tables 1.2 and 1.3).

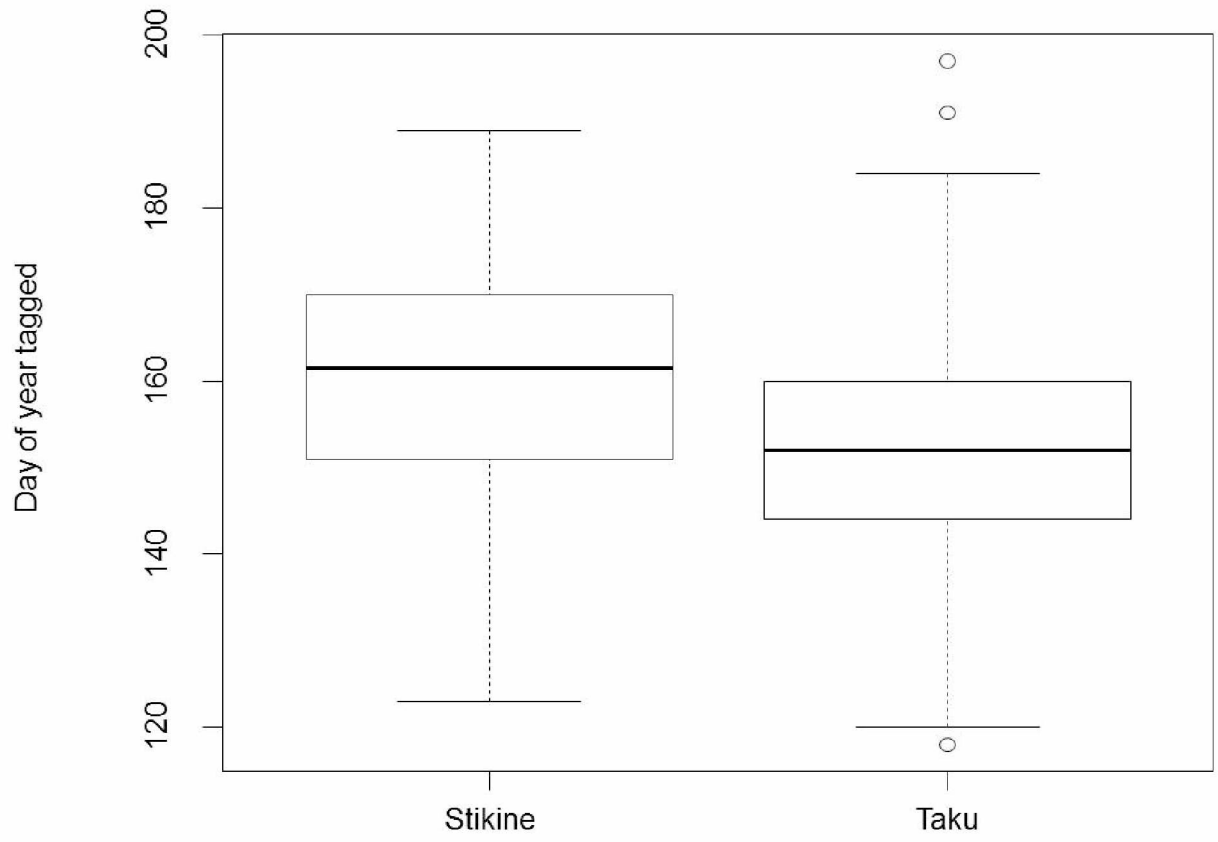

Figure 1. 3. Tagging dates (day of year after 1 January) of Chinook Salmon in the Stikine and Taku Rivers, Alaska. The box dimensions represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles, the solid lines inside the boxes are the medians, and dots represent outliers.

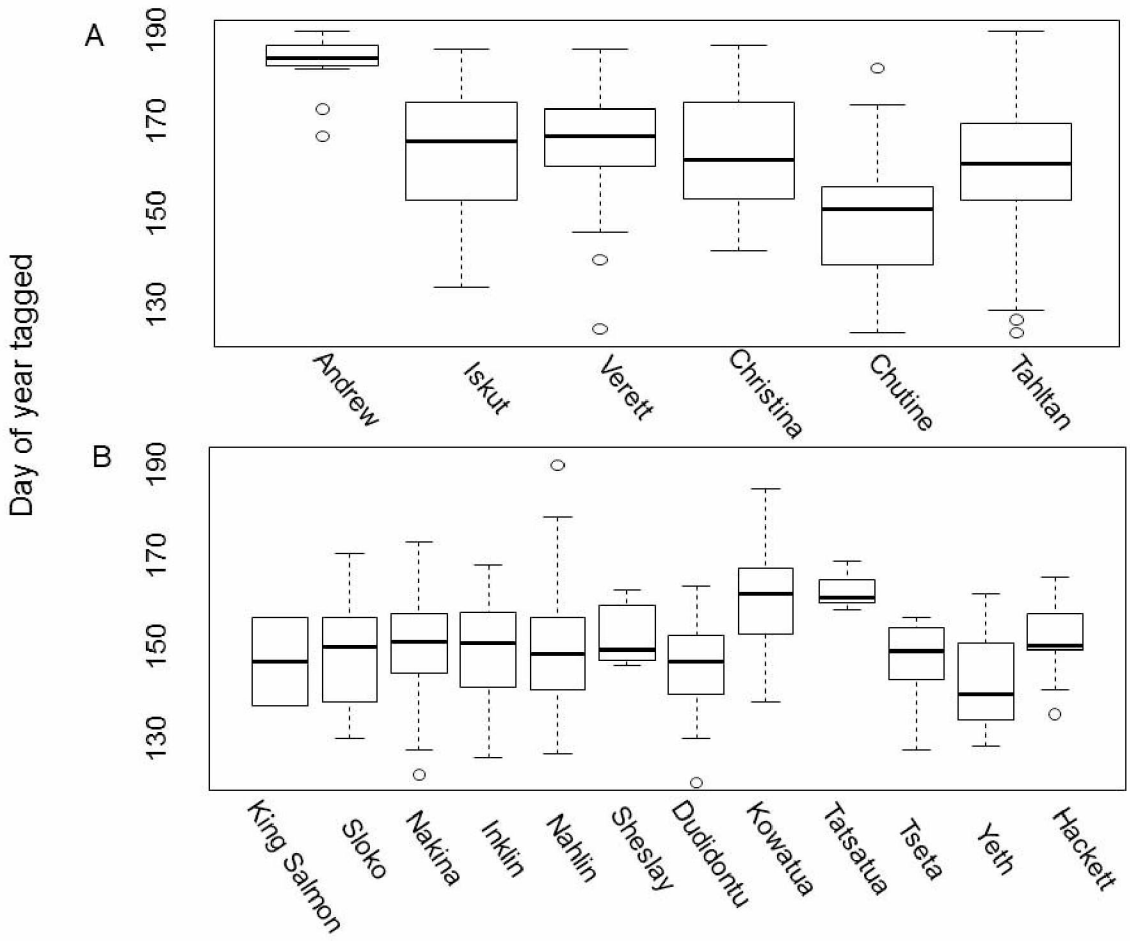

Figure 1. 4. Day of year tagged for Chinook Salmon by tributaries within the Stikine (A) and Taku (B) River basins, Alaska. The box dimensions represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles, the solid lines inside the boxes are the medians, and dots represent outliers.

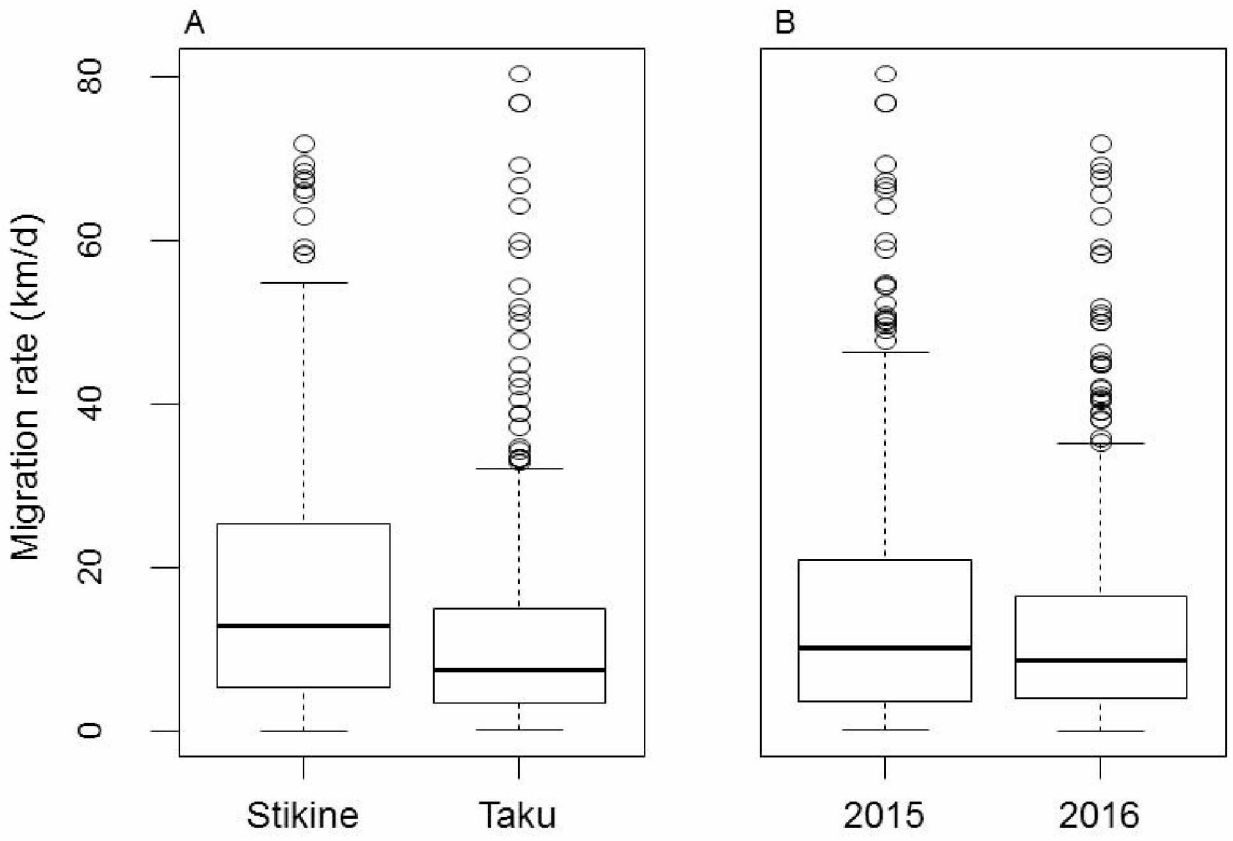

Figure 1. 5. Migration rates (km/d) for Chinook Salmon in the Stikine and Taku Rivers (A), and for fish tagged in 2015 and 2016 (B). The box dimensions represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles, the solid lines inside the boxes are the medians, and dots represent outliers.

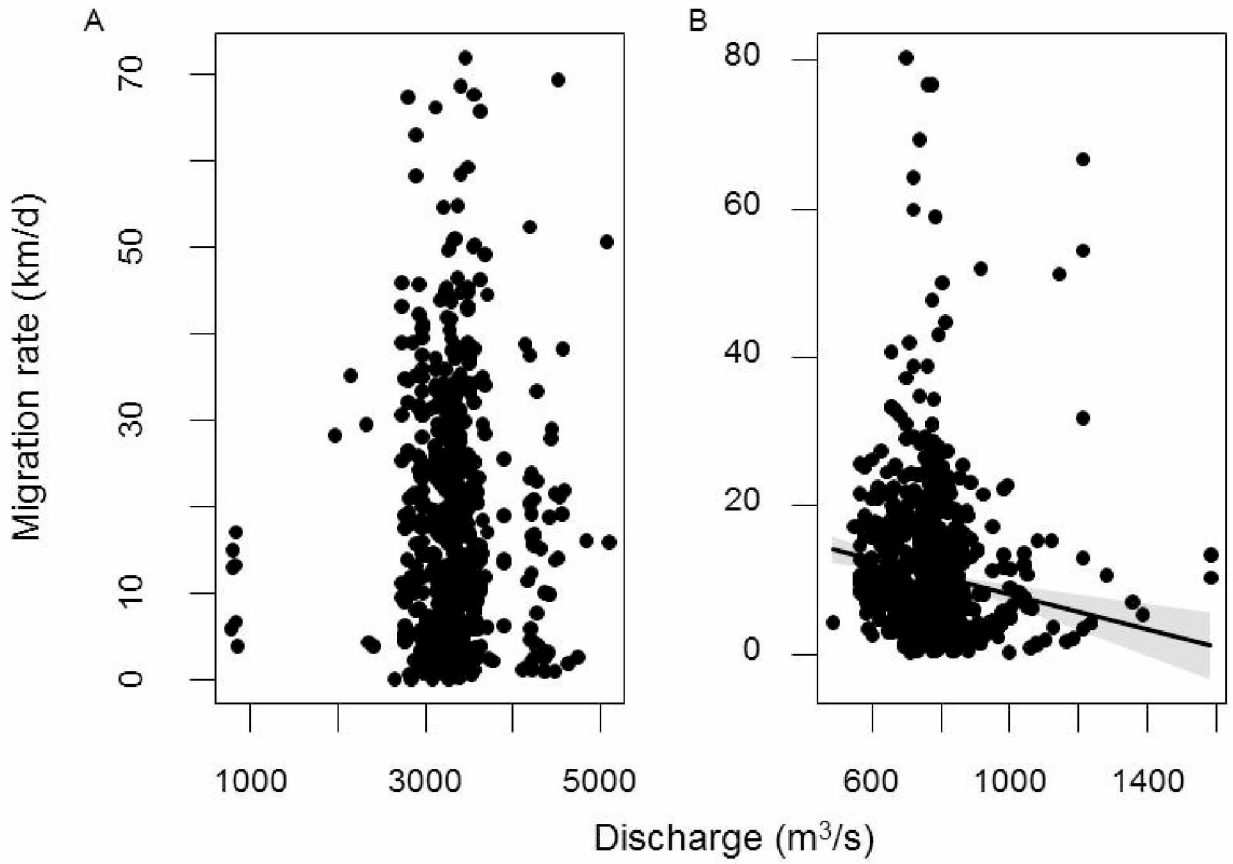

Figure 1. 6. Relationship between migration rates (km/d) of individual Stikine (A) and Taku (B) River Chinook Salmon and river discharge (m^3/s). Lines (± 95% confidence interval bands) are the estimated relationship from a linear mixed model (Tables 1.4 and 1.5).

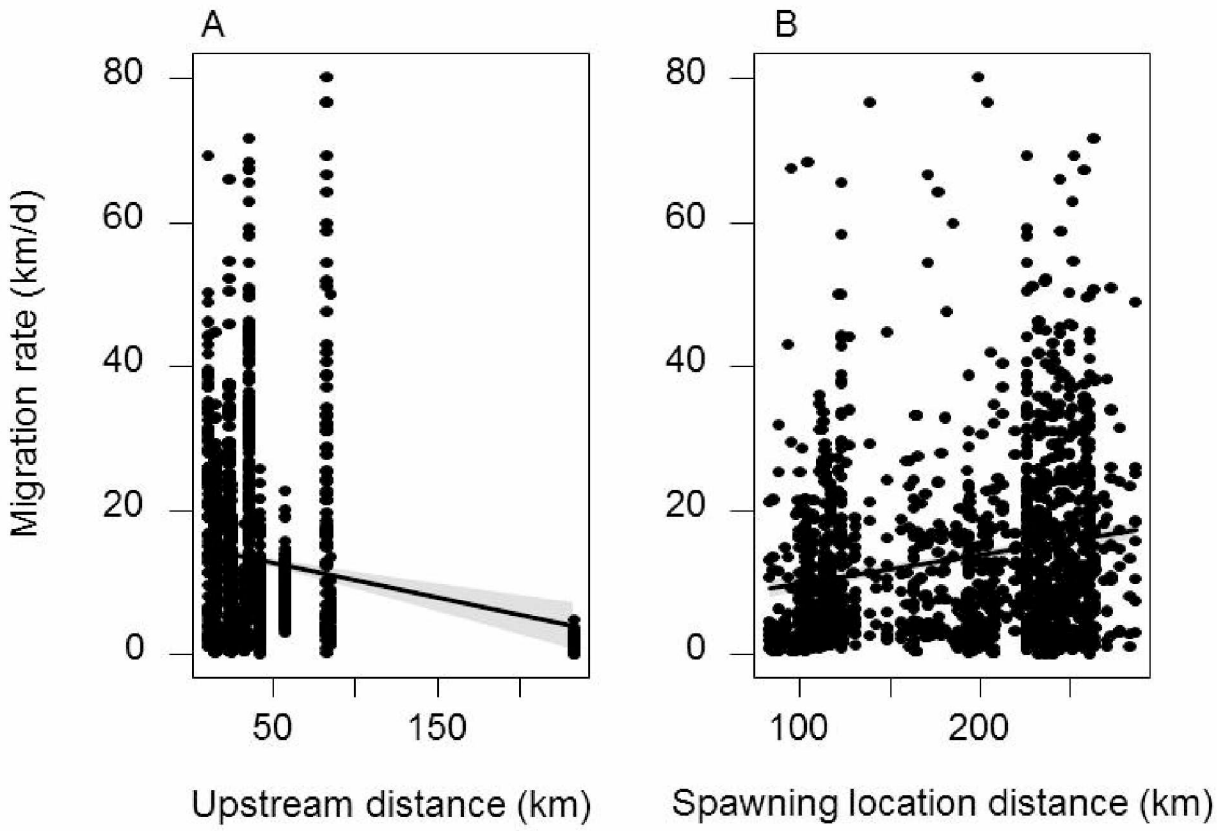

Figure 1. 7. Migration rates (km/d) for individual Chinook Salmon from the Stikine and Taku Rivers (points) versus (A) upstream distance (km) at detection (i.e., tower location distance), and (B) spawning location distance. Lines (± 95% confidence interval bands) are the estimated relationship from a linear mixed model (Tables 1.4 and 1.5).

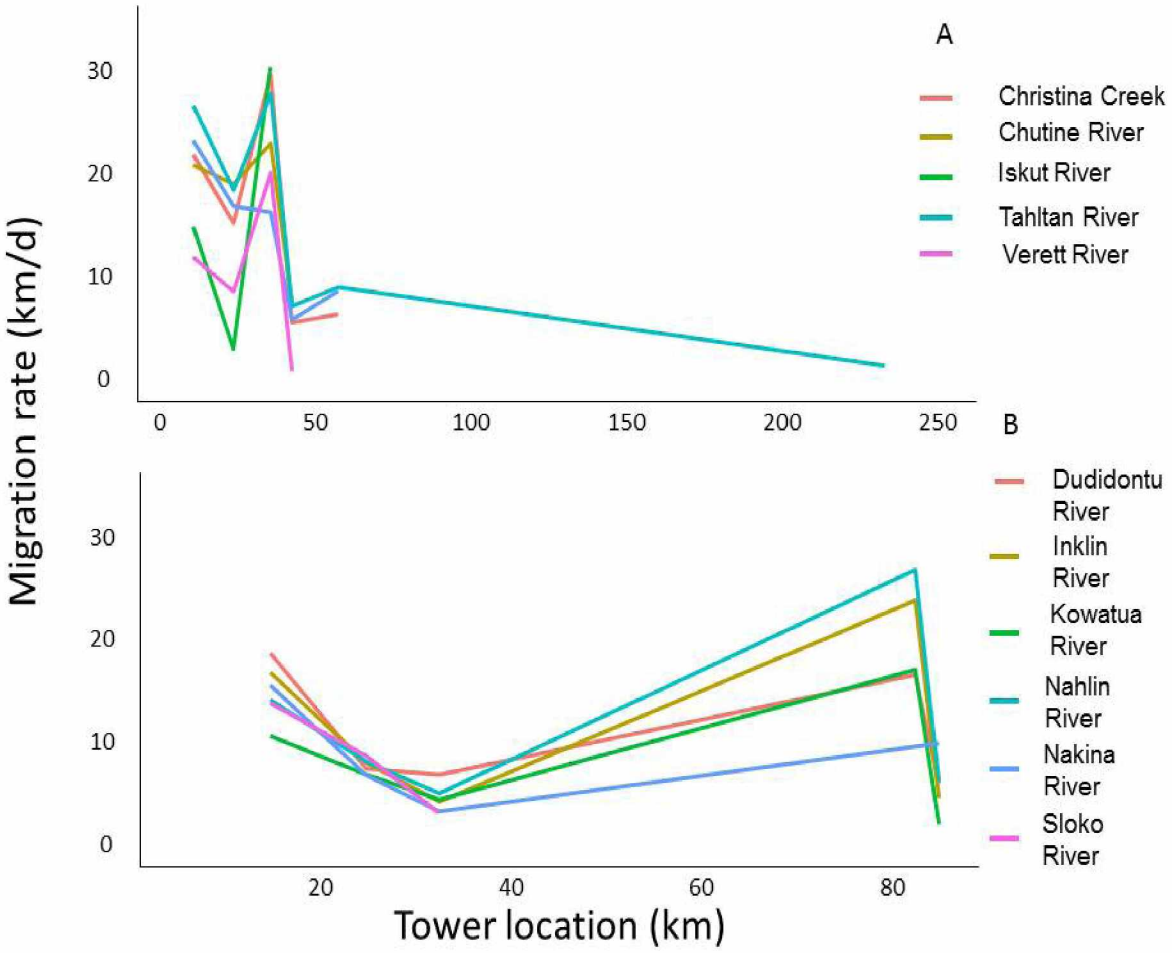

Figure 1. 8. Migration rates averaged across all tagged Chinook Salmon by tributary from (A) the Stikine River and (B) the Taku River as a function of upstream distance (km) at detection (i.e. tower location; x-axis). Colors indicate different tributary stocks.

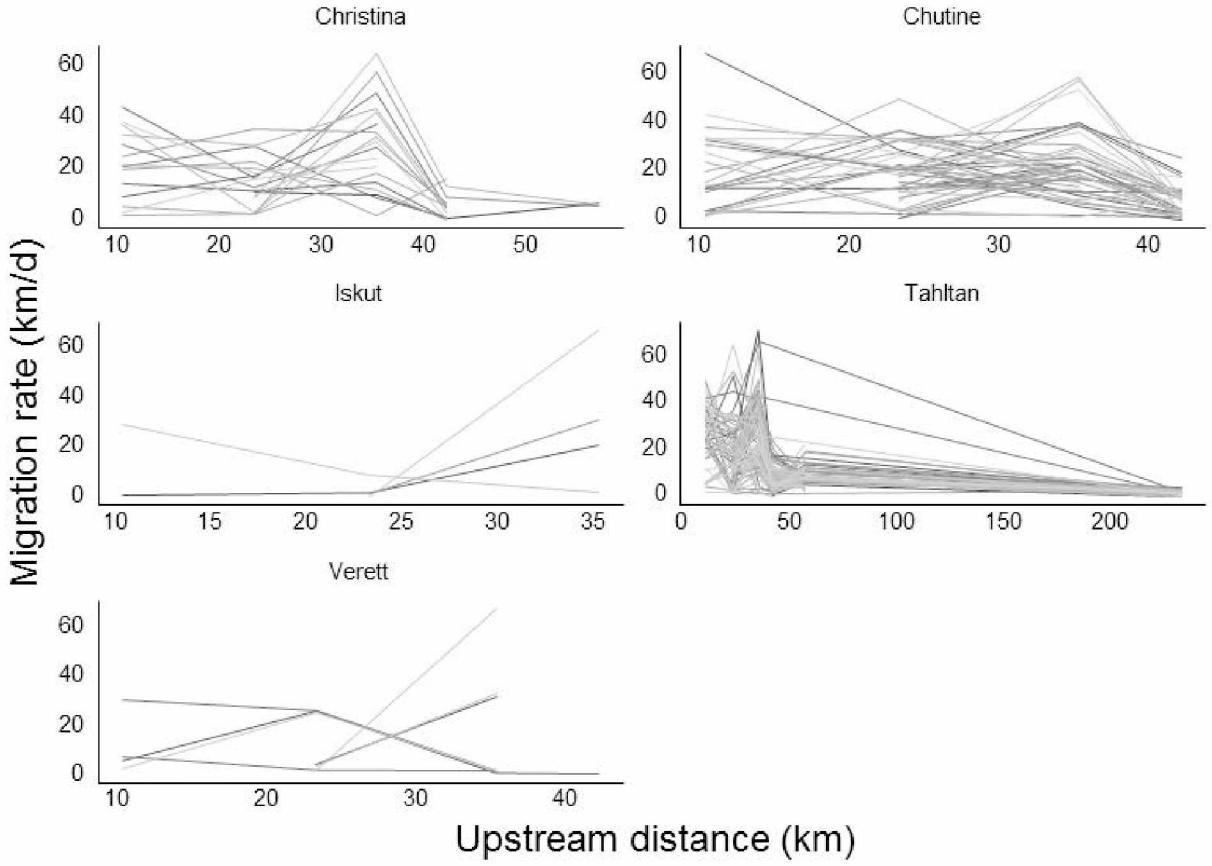

Figure 1. 9. Migration rates (km/d) of individual tagged Chinook Salmon (lines) by tributary from the Stikine River as a function of upstream distance (km) at detection (i.e. tower location; x-axis).

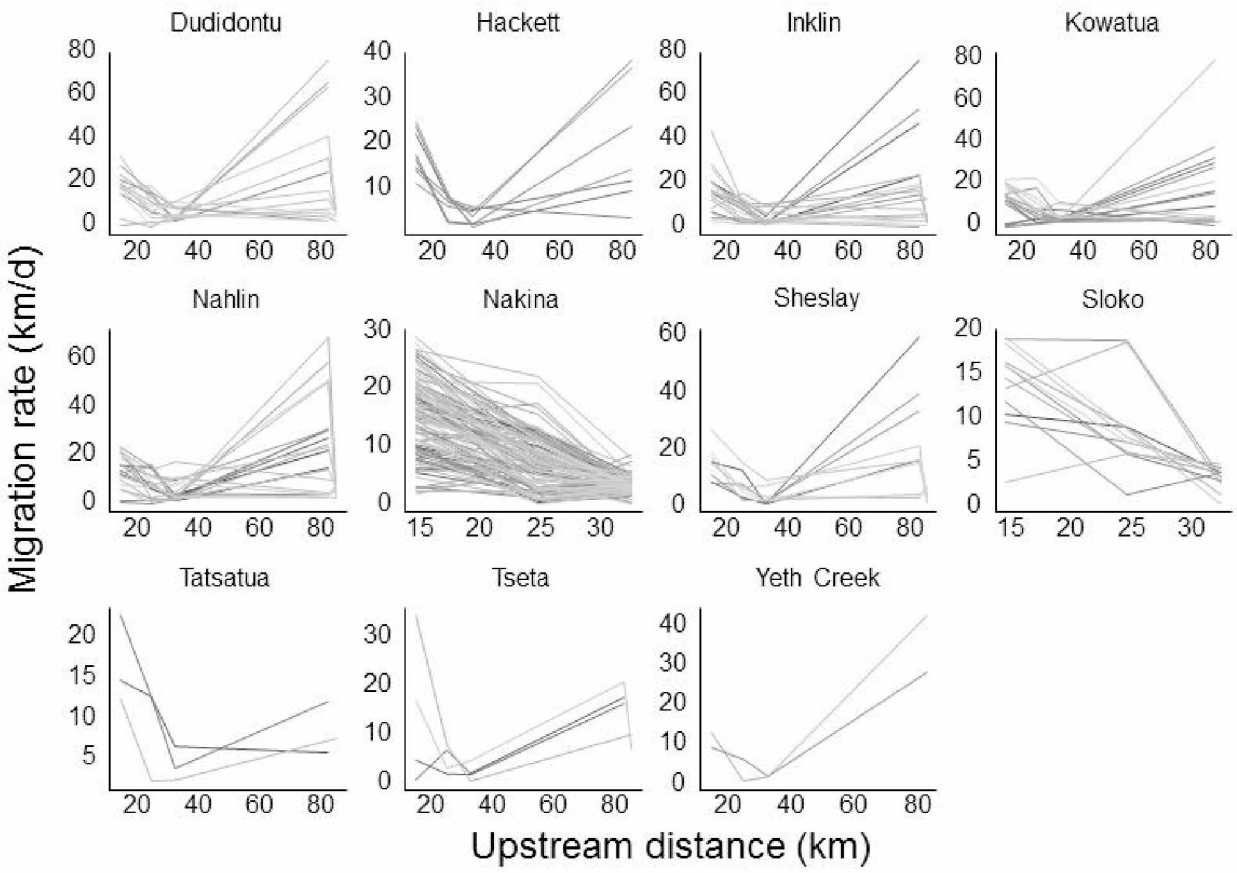

Figure 1. 10. Migration rates (km/d) for individual tagged Chinook Salmon (lines) by tributary from the Taku River as a function of upstream distance (km) at detection (i.e. tower location; x-axis).

Table 1. 1. Number of Chinook Salmon (mid eye to fork length ≥ 660 mm) tagged (*N*) and tracked to a final location (*n*) in each river by year. Mean, maximum, minimum and standard deviation mid eye to fork length (mm) and sex (M/F) are shown.

Year	River	*N*	*n*	M	F	Mean	Min	Max	SD
2015	Stikine	300	176	81	219	778.0	660	975	58.96
2015	Taku	316	253	152	191	752.8	660	950	60.34
2016	Stikine	170	94	59	112	766.2	660	980	63.26
2016	Taku	238	150	73	165	758.4	660	970	58.25

Table 1. 2. Summary of model selection statistics for top migration timing models ($w_i > 0.05$) for Chinook Salmon from the Taku and Stikine Rivers, Alaska. SD = spawning distance (km), Dish = discharge (m^3/s), Len = length (mid eye to fork length; mm), K = the number of model parameters, L-L = the log-likelihood, ΔAIC = the difference in the Akaike information criterion value (AIC) for a particular model when compared to the top model, and w_i = Akaike weight.

Model	K	L-L	AIC	ΔAIC	w_i
SD+River	4	-2674.85	5357.76	0.00	0.20
SD+Dish+River+Year	6	-2673.05	5358.24	0.47	0.16
SD+Dish+River+Sex+Year	7	-2672.21	5358.59	0.83	0.13
SD+Dish+Len+River+Sex	7	-2672.28	5358.73	0.97	0.12
SD+Dish+Len+River+Sex+Year (global)	8	-2671.26	5358.73	0.97	0.12
SD+Dish+Len+River+Year	7	-2672.33	5358.83	1.06	0.12
SD+Len+River+Sex+Year	7	-2672.66	5359.48	1.72	0.08

Table 1. 3. Model-averaged parameter estimates, relative variable importance, and lower and upper 90% unconditional confidence intervals (CIs) for covariates predicting migration timing of Chinook Salmon in the Stikine and Taku Rivers, Alaska. Estimates were derived from the confidence set of models with 95% of the Akaike weight (Table 1.2).

Covariate	Parameter Estimate	Relative Importance	Lower 90% CI	Upper 90% CI
Spawning Distance	-0.04	1.00	-0.05	-0.03
River	-6.78	0.93	-11.67	-1.88
Discharge	3.14e-5	0.72	-2.10e-06	9.12e-05
Year	0.95	0.66	-0.36	3.24
Sex	0.74	0.51	-0.26	3.21
Length	-0.01	0.50	-0.03	2.97e-03

Table 1. 4. Summary of model selection statistics for top migration rate models for Chinook Salmon from the Stikine and Taku Rivers, Alaska. SD= spawning distance (km), Dish= discharge (m^3/s), Len = fish length (MEF; mm), UD = upstream distance at detection (km), Riv = river, DT = day of year tagged, K = the number of model parameters, L-L = the log-likelihood, ΔAIC = the difference in the Akaike information criterion value (AIC) for a particular model when compared to the top model, and w_i = Akaike weight.

Model	K	L-L	AIC	ΔAIC	w_i
Year+Riv+Dish+SD+Sex+UD	9	-5940.04	11898.08	0.00	0.45
Year+Riv+Dish+SD+Len+Sex+UD	10	-5939.85	11899.70	1.62	0.20
Year+Riv+DT+Dish+SD+Sex+UD	10	-5940.18	11900.37	2.29	0.14
Year+Riv+SD+UD	9	-5941.87	11901.73	3.65	0.07
Year+Riv+DT+Dish+SD+UD	11	-5940.03	11902.06	3.98	0.06
Year+Riv+DT+Dish+SD+Length+Sex+UD (global)	10	-5941.42	11902.83	4.75	0.04

Table 1. 5. Model-averaged parameter estimates, relative variable importance and lower and upper 90% unconditional confidence intervals (CIs) for covariates predicting migration rates of Chinook Salmon in the Stikine and Taku Rivers, Alaska. Estimates are derived from the confidence set of models with 95% of the Akaike weight (Table 1.4).

Covariate	Parameter Estimate	Relative Importance	Lower 90% CI	Upper 90% CI
Year	-1.35	1.00	-2.38	-0.31
River	-9.86	1.00	-14.09	-5.63
Discharge	-2.39	0.96	-4.45	-0.32
Spawning Distance	1.54	1.00	0.93	2.15
Sex	-0.87	0.86	-2.02	0.12
Upstream Distance	-2.55	1.00	-3.07	-2.03
Length	-0.09	0.31	-0.82	0.24
Day Tagged	0.04	0.33	-0.37	0.64

Chapter 2: Patterns and modeling of energetic status in Alaska Chinook Salmon[2]

ABSTRACT

Adult Pacific Salmon *Oncorhynchus spp.* undertake energetically demanding migrations wherein they must have adequate lipid reserves to survive to spawning locations and reproduce. Energetic status measurements can provide insight into the lipid stores these fish have available for their upstream migrations, and methods attempting to measure lipid content non-lethally are useful for managers seeking to understand how energetic status of fish affects behavior and mortality. The ability to non-lethally monitor the energetic status of salmon populations may be especially important in light of population declines and threats from climate change and habitat alteration. Bioelectrical impedance analysis (BIA) is one such method to accurately and non-lethally assess energetic status in fish, but species-specific models are lacking for many salmon species. In this study, 129 Chinook Salmon *Oncorhynchus tshawytscha* were sampled from four populations in Alaska to examine variation in energetic status and build predictive BIA models for this species. Total body percent lipid and percent water were estimated using proximate analysis and the best BIA predictive model was determined for two measurement devices (Quantum II [Q2] and Certified Quality Reader [CQR]). We also tested if BIA models are generalizable across similar species (e.g., Chum Salmon *Oncorhynchus keta*) and examined the feasibility of integrating BIA measurements into field studies. Populations sampled at the beginning of their freshwater spawning migration had higher percent lipid than those near the spawning grounds ($P < 0.001$), and total percent lipid and water were precisely predicted based on BIA measurements ($R^2 = 0.82$; $R^2 = 0.78$, respectively) from the Q2 device. Models based on CQR measurements, and

[2]Neuneker, K.R., J.A. Falke, M.K. Cox, F.J. Margraf, K.J. Hartman, and J.V. Nichols. Patterns and modelling of energetic status in Alaska Chinook Salmon. Formatted for *North American Journal of Fisheries Management.*

between-species, were less precise ($R^2 < 0.71$), but we found that the BIA technique was easily implemented into a Chinook Salmon radiotagging study on a remote Southeast Alaska river. Our results indicate that integration of BIA into population monitoring could be a valuable tool to assess energetic status of Chinook Salmon across space and through time. Such knowledge can contribute towards improved management of this sensitive species by allowing mangers to set harvest limits and management goals based on allowing fish to maintain or increase their energetic status at a level that allows them to successfully migrate to their spawning locations and reproduce.

INTRODUCTION

To survive, individual fish must maintain a balance between energetic stores gained through feeding and energy used during growth, reproduction, and movement (Brett 1995; Quinn 2005). The study and estimation of fish energetics and growth are an aspect of fish biology that is often used in management practices (Brandt and Hartman 1993; Hansen et al. 1993), and energetic status (e.g., lipid, protein, water content) is an important indicator of fish body condition (Bolger and Connolly 1989). Lipid stores make up the majority of energetic fuel for Pacific Salmon *Oncorhynchus spp*. and are critical for upstream migrations as semelparous adults stop feeding once they enter freshwater on their migration to spawning grounds (Brett 1995; Quinn 2005; Mesa and Magie 2006). As fish use these energy stores, they replace lipids with water to maintain their body shape and use protein stores after lipid reserves have been depleted (Hartman and Margraf 2008; Stolarski et al. 2014). Lipid content in spawning salmon varies by sex and spawning location distance owing to differences in energy needs (Quinn 2005; Minke-Martin 2017). Female salmon have a higher energetic demand than males due to the need to produce energy rich eggs and thus require more lipid stores during spawning, so that

individuals with more challenging migrations often have fewer and smaller eggs than those with shorter migrations (Kinnison et al. 2001; Hearsey and Kinzinger 2015). Whereas egg characteristics in females can change depending on the energetic costs to reach spawning sites, males divert any lipid stores that are not used for swimming into secondary sexual characteristics and competitive interactions (Kinnison et al. 2003; Mesa and Magie 2006). Therefore, energetic status of individuals during spawning migrations is an important factor to consider when monitoring stock health and may play a large role in successful spawning activities.

Measuring changes in energetic status in the field is often performed by measuring the length and mass of a fish where heavier fish at a given length are assumed to be in better condition (i.e., have higher energy reserves; Pope and Kruse 2007). Condition indices such as Fulton's condition factor (K), relative weight (W_r; Neumann et al. 2013), and analysis of residuals from species- or population-specific length-mass regressions (Bentley and Schindler 2013) can be calculated from length and mass measurements. Such condition indices work well for relative comparisons of growth rates within a population at a single point in time (Blackwell et al. 2000). However, morphological condition indices have been shown be unable to distinguish lipid and water weight from one another, and are not representative of energetic status (Sutton et al. 2000, Simpkins et al. 2003, Trudel et al. 2005). Proximate composition (PC) analysis (AOAC 2005) has long been used to estimate energetic status of individual fish in a laboratory setting, and although highly accurate, the technique is lethal (Hartman et al. 2015). Thus, PC methods may be inappropriate for sensitive populations that are experiencing declines, listed as a species of concern, or endangered. Furthermore, repeated measurements on an individual over time are not possible using PC methods. Development of precise and accurate methods to measure and monitor the energetic status of individual fish in the field are needed to

assess how fish respond energetically to environmental change, and quantify energetic differences within and among populations.

Bioelectrical impedance analysis (BIA) is a non-lethal alternative to PC and condition indices that uses the properties of electrical conductivity to predict indices of energy density in fishes, such as total body lipids and water (Kyle et al. 2004). A device is used to measure electrical properties (e.g., resistance and reactance) using electrodes. As lipid is nonconductive, resistance measurements are a measure of lipid content, whereas reactance is indicative of the volume of healthy cells in the body. Electrical metrics are then used to build species-specific models to predict energetic status via calibration with laboratory PC estimates (Cox and Hartman 2005; Cox and Heintz 2009; Stolarski et al. 2014). This method has been shown to be accurate and precise when estimating fish energetic status in a number of studies where an adequate sample size and total lipid range of fish have been used to build models (Hartman et al. 2015). Although there is some evidence that BIA predictive models are transferrable among closely related species (e.g., within families; Duncan 2008), the utility of predicting energetic status among large-bodied salmonid (Salmon and Trout) species, many of which are sensitive or endangered, remains unknown. As such, the ability to non-lethally predict energetic status based on previously established models may be highly useful for conservation and monitoring of sensitive populations or species.

Chinook Salmon provide invaluable ecological, economic and cultural resources for Alaska; many of these populations are currently in decline, yet mechanisms driving these declines are not completely understood (Quinn 2005; Clark et al. 2006; Bottom et al. 2009; ADF&G 2013). Additionally, Alaska rivers and streams are expected to experience increases in temperature and discharge variability due to climate change (van Vliet et al. 2013; Shanley and

Albert 2014; Sloat et al. 2016). This poses threats to salmon migrating upstream, where energy expenditure may increase owing to changing flow regimes and higher temperatures (Keefer et al. 2004, 2014). In addition, some Alaska salmon populations have exhibited trends toward declining body size (Lewis et al. 2015), which could indicate decreased body condition and energetic status during spawning migrations (Kilduff et al. 2015), which may have far-reaching implications. Although it is clearly important to understand variation in energetic status among Chinook salmon populations, many Alaska river systems are very remote and logistics for monitoring these wild populations are challenging. Therefore, development of techniques to accurately and non-lethally monitor energetic status in remote systems using quick, simple methods will be important for developing more knowledgeable and directed future management strategies.

The overall goal of this study was to develop BIA models for Chinook Salmon to provide fisheries managers and researchers with tools to non-lethally predict the energetic status of this fish. Such methods may be particularly useful in light of the sensitive status of Chinook Salmon populations in Alaska and elsewhere. Our specific objectives were to 1) estimate and examine among-population differences in proximate composition (lipid, water, protein) for four Alaska Chinook Salmon populations, 2) build and evaluate predictive models based on the relationship between proximate components and BIA electrical measurements for the four populations, 3) assess the utility of among-species prediction of energetic status using Chinook Salmon and Chum Salmon *Oncorhynchus keta* BIA models, and 4) quantify relationships among BIA-predicted energetic status, sex, and spawning location for a remote Southeast Alaska Chinook Salmon population to evaluate field based estimates of BIA in a remote setting.

METHODS

Sample Sites.— Chinook Salmon were lethally sampled and collected for BIA model development using drift gill nets, electrofishing, and from a hatchery facility at four locations across Alaska that included the mouth of the Yukon River near Emmonak (62.776° N, 164.555° W) , the mouth of the Nushagak River near Dillingham (59.023° N, 158.443° W), the Chena River near Fairbanks (64.963° N, 146.238° W), and Whitman Lake Hatchery near Ketchikan (55.328° N, 131.529° W; Figure 2.1). The Yukon River is the largest river in Alaska, with a watershed area of 832,700 km^2 and a Chinook Salmon abundance estimate of 100,000 – 400,000 fish (ADF&G 2013). The Nushagak River (34,700 km^2) is the largest producer of Chinook Salmon in southwestern Alaska, with an estimated average abundance of 156,000 fish. The Chena River (5,300 km^2) is a tributary of the Tanana River, which flows into the Yukon River and is located approximately 1,300 km from the Yukon River mouth. The Chena River contains one of the largest Yukon River drainage Chinook Salmon spawning populations, with abundance estimates ranging from 2,000 – 6,400 individuals (Savereide and Huang 2014). Whitman Lake Hatchery is one of the largest hatcheries operating in southeast Alaska under the Southern Southeast Regional Aquaculture Association (SSRAA). Chinook Salmon broodstock for this hatchery is sourced from the nearby Chickamin River (Stopha 2016). Between the years of 1980 and 2011, returns of Chinook Salmon to the hatchery have ranged from 380 – 26,424 individuals. Our study sites were selected to ensure capture of individuals that represent a range of total body lipid conditions as suggested by Hartman et al. (2015). We anticipated that fish collected near their freshwater entry point (Nushagak and Yukon Rivers) would have high lipid content, and those collected at or near terminal locations (spawning grounds or hatchery; Chena River, Whitman Lake Hatchery) would have moderate or low lipid content.

To investigate between-species predictive ability of BIA models, Chum Salmon were lethally collected from the Yukon River at Emmonak, AK and near spawning locations at the confluence of the Delta and Tanana Rivers (64.156° N, 145.852° W; Margraf et al. 2005; Cox and Heintz 2009; Hartman et al. 2015) to maximize the range of lipid content. The Delta River supports 11 – 24% of the fall spawning Chum Salmon in the upper Tanana River basin with a mean spawning abundance of 14,563 fish between 1974 and 2009 (Borba et al. 2009).

Chinook Salmon were non-lethally sampled from the Stikine River during a radiotagging study (Chapter 1) to investigate how energetic status differs between sexes and spawning locations and to assess the feasibility of BIA methods in the field. The Stikine River is the largest transboundary (flowing from Canada into the United States) river in southeast Alaska with a watershed area of 51,593 km^2 and has the second highest Chinook Salmon abundance in the region, with an spawning abundance estimate average of 25,000 large individuals returning to the River. Chinook Salmon were captured near the vicinity of Kakwan point (56.691° N, 132.226° W) located near the mouth of the Stikine River during an ongoing Alaska Department of Fish and Game (ADF&G) mark – recapture project (Richards et al. 2015).

Field Methods.— Upon capture, Chinook Salmon used for BIA model development from Emmonak, the Nushagak River, Chena River and Whitman Lake Hatchery, were sacrificed via cranial concussion and then biological and electrical measurements were taken. Immediately after death, each fish was blotted dry and placed on a non-conductive surface. Individuals were measured for mid eye to fork (MEF; mm), post orbital to hyperal (POH), mid eye to hyperal (MEH) and fork (FL) lengths, classified to sex, and an internal temperature was taken through the vent to the nearest 0.1°C using a meat thermometer. To investigate electrical measurement variability within and among BIA devices, three replicate resistance and reactance measurements

were taken on the dorsal side using the Seafood Analytics Certified Quality Reader (CQR) device and at the dorsal midline (DML) and ventral total length (VTL) positions (Figure 2.2; Hafs and Hartman 2011) with the RJL systems Quantum II Analyzer (Q2; RJL Systems Detroit, Michigan; Figure 2.3). These positions were standardized to match previous BIA work (Margraf et al. 2005). The distance between electrodes was measured to the nearest millimeter for measurements made with the Q2 meter. Fish were weighed to the nearest 0.1 kilogram (kg), individually tagged for identification, and immediately transported to a freezer for return to the laboratory for proximate analysis.

Chinook Salmon were sampled for resistance and reactance values on the Stikine River during annual ADF&G tagging studies in 2015 and 2016. Upon capture of a Chinook Salmon on the Stikine River, as indicated by a bobbing motion of gillnet corks, fish were placed into a neoprene cradle and immersed in a live well containing fresh river water (Richards et al. 2015). Fish deemed to be healthy (e.g., no bleeding injuries, loss of color or equilibrium), were then measured (MEF; mm), classified to sex based on morphology, and the CQR device was used to collect dorsal side BIA measurements as described above. Fish were then released alive back into the river.

Laboratory Methods.— After collection for BIA analysis of Chinook Salmon from Emmonak, the Nushagak River, Chena River and Whitman Hatchery, fish were homogenized using an industrial grinder. From this mixture, six 50 mL subsamples were collected per fish. One subsample from each fish was sent to the University of Idaho, Hagerman Station for proximate composition analysis to determine percent water content, as well as lipid, protein and ash content as a percentage of dry weight (AOAC 1990). These measurements were taken in triplicate, and a mean of the values was used for model development (Cox and Hartman 2005).

Statistical Methods.— We compared percent lipid, water, protein, and ash as determined by proximate composition analysis among the four sample locations (Emmonak, Nushagak, Chena and Whitman) and between sexes using an analysis of variance test (ANOVA). An initial two-way ANOVA between sex and location resulted in no significant interaction, so we ran a two way ANOVA without the interaction effect to assess differences among sample locations, and between sexes. If significant differences ($\alpha = 0.05$) were detected, a Tukey's HSD post-hoc test was used for multiple comparisons.

Averaged resistance and reactance values from the CQR and Quantum II (Q2) devices were corrected for fish temperature with equations developed in a previous study on Chum Salmon and were used to calculate a variety of electrical parameters to develop a predictive model for percent lipid and percent dry mass (water) (Margraf et al. 2005; Hartman et al. 2015; Table 2.1). These electrical parameters were divided into groups of measurements by the device with which they were collected (CQR or Q2) to compare precision between the two devices, and then added to data sets that included biological variables collected from fish (e.g., length, weight, sex). Models were fit to the two observed responses (percent dry lipid and water) as a function of the biological and electrical variables using ordinary least squares (OLS) regression in the statistical package R (R Development Core Team 2012; Stolarski et al. 2014). The Mallows' C_p score was estimated for all subsets of the models using the R package leaps, and models were organized by length (i.e., number of covariates; Lumley 2017). The models with the lowest Mallows' C_p score for each length were retained for further analysis. Four candidate model sets were created: 1) a model containing length and weight only, 2) combined lateral, ventral and biological measurements, 3) lateral and biological measurements only and 4) ventral and biological measurements only. Model sets were developed to investigate if both lateral and

ventral measurements are needed. Akaike's Information Criterion corrected for small sample size (AIC_c) was used to select the best model that predicted percent water and lipid (Burnham and Anderson 2002).

Because Chinook Salmon and Chum Salmon are congenerics and similar in size and body shape, we investigated whether BIA model parameters from one species were interchangeable with the other, based on the top Chinook Salmon BIA model (see Results) and a BIA model parameterized for Chum Salmon (Hartman et al. 2015). We compared R^2 values and root mean squared error (RMSE) between 1) Chum Salmon coefficients with Chinook Salmon data, 2) Chinook Salmon coefficients with Chum Salmon data, 3) each species model with their own coefficients, and 4) a model with Chinook and Chum Salmon data combined.

Finally, we used the top CQR device Chinook Salmon BIA model to predict percent lipid and water of individuals captured from the Stikine River during a tagging study (Chapter 1). Predicted percent lipid and water content were compared separately between sexes and among spawning locations using ANOVA and Tukey's HSD test as described above. Spawning locations were determined by tracking radio telemetry tagged Chinook Salmon to their spawning tributaries during aerial telemetry surveys, and grouping fish into spawning locations based on these tributaries (Chapter 1).

RESULTS

A total of 129 Chinook Salmon were lethally collected for BIA model development (Table 2.2), of which 80 were male and 49 were female. Fork lengths were 541 – 998 mm (mean = 796.3 mm, SD = 99.7).

Proximate Composition

Water and lipid content for Chinook Salmon ranged from 49.26 to 77.03% (mean = 65.76%, SD = 5.02) and 5.82% to 51.02% (mean = 30.23%, SD = 12.54) respectively. Percent protein was 43.98 to 87.03% (mean = 62.76%, SD = 10.92) and percent ash ranged from 3.81 to 12.95% (mean = 7.72%, SD = 1.8). Chinook Salmon proximate components differed among the four populations and between sexes (Figure 2.4; Figure 2.5). Mean water content (%) differed among locations (ANOVA: $F = 129.4$, df = 3, $P < 0.001$) though no differences were found between the Emmonak and Nushagak populations (Tukeys HSD: $P = 0.14$) or Chena and Whitman populations ($P = 0.13$), where Emmonak and Nushagak had a lower water content than Chena and Whitman. Percent lipid content differed among the four populations ($F = 200.7$, df = 3, $P < 0.001$), with the Emmonak population having the highest and Whitman the lowest ($P < 0.001$). Protein differed among three populations ($F = 192.9$, df = 3, $P < 0.001$) with Whitman and Chena having similar means ($P = 0.58$), and a higher protein content than fish from the Nushagak River followed by Emmonak. Percent ash differed among all four populations, where Whitman and Emmonak had the highest and lowest content ($F = 62.02$, df = 3, $P < 0.001$), respectively. Percent lipid ($F = 0.17$, df = 1, $P = 0.69$), percent protein ($F = 2.18$, df = 1, $P = 0.16$), and percent ash ($F = 0.56$, df = 1, $P = 0.47$) did not differ between sexes, but percent water was significantly different with males having a higher water content than females ($F = 11.08$, df = 1, $P = 0.0018$).

BIA Model Development

The top model for the Q2 device explained 82% of the total variability between observed and predicted percent lipid content and 78% of the total variability between observed and predicted percent water content (Table 2.3; Figure 2.6). The top models for the CQR device

explained less (61%) of the variability in lipid content and of the variability (71%) in water content (Table 2.4; Figure 2.7). Model coefficients for the top performing model for the Q2 device included parameters from both ventral and dorsal electrical measurements as well as biological variables, while the top performing model for the CQR device was the global model (Table 2.5; Table 2.6).

BIA Model Application

Predictions of lipid and water content for Chinook and Chum Salmon using BIA models developed for the other species produced lower R^2 and higher RMSE values than Chinook- (Chinook – Chinook) or Chum- (Chum – Chum) specific models (Table 2.7). Predictions of lipid content in Chinook Salmon using the coefficients derived from the Chum Salmon (Chum – Chinook) model explained the lowest amount of variability in percent lipid from proximate analysis and had the highest RMSE when compared to the other models tested ($R^2 = 0.53$; RMSE = 19.47). The model predicting Chum Salmon energetic status using coefficients from the Chinook Salmon (Chinook – Chum) model had a higher R^2 value and lower RMSE ($R^2 = 0.63$; RMSE = 7.69) than the Chinook – Chum model, but did not perform as well as the Chum – Chum model ($R^2 = 0.93$; RMSE = 3.21) or the Chinook – Chinook model ($R^2 = 0.78$; RMSE = 2.43; Table 2.3). There was a similar pattern in the predictions of water content, where the Chinook – Chum model had the lowest R^2 and highest RMSE values, and the Chum – Chinook model had R^2 and RMSE values between those of the Chinook – Chum and the same species models. The model using combined Chinook and Chum Salmon data produced R^2 (lipid = 0.84; water = 0.81) and RMSE (lipid = 4.99; water = 2.48) values similar to those of the Chinook – Chinook and Chum – Chum models.

Lipid and water content of Chinook Salmon from the Stikine River (N = 127, males = 43, females = 84) were predicted using with the model developed for the CQR device (Table 2.4; Table 2.6). This model predicted that percent total lipids for this population ranged from 9.5 to 41.5% (mean = 20.62%, SD = 3.26) and 61.82 to 78.58% water (mean = 73.72%, SD = 2.05), with lipid contents of 40% of individuals being in the 10–20% range and 57% in the 20–30% range. The majority (96%) of individuals ranged from 70 to 80% water content. The ANOVA analysis indicated no differences between sexes (F = 0.27, df = 1, P = 0.61; F = 0.52, df = 1, P = 0.76) or among the six spawning locations determined using radio telemetry (F = 1.38, df = 5, P = 0.24; F = 0.29, df = 1, P = 0.59; Chapter 1) in percent lipid and water, respectively.

DISCUSSION

The results of this study provide fisheries researchers and managers with tools to develop research and monitoring projects focused on monitoring trends in energetic status for important Pacific salmon populations, including species in remote rivers. The ability to predict energetic status in fish accurately and non-lethally can be an important aspect of management, energetic status can be correlated to the relative reproductive capacity of a population, pre-spawn mortality rate, and the ability of fish to survive periods of low food abundance (Biro et al. 2004; Mesa and Magie 2006). This study examined energetic status among Chinook Salmon populations in remote locations around Alaska, and offers a new model for predicting energetic status in Chinook Salmon. We found that the BIA model using the Q2 device accurately predicted Chinook Salmon body condition, and that BIA devices were able to be successfully implemented into Chinook Salmon studies on a remote Alaskan river. This study found some evidence that BIA models could be generalized between similar species, but improvements should be made in future studies to gain a better understanding of the ability to transfer models between species.

Proximate Composition

Chinook Salmon in this study displayed differences in energetic status based on whether they were in the initial or final stages of their spawning migration. Similar to our results, other studies have documented decreases in energetic status (decreased lipid content and increased water content) over the spawning migration, as fish use energy reserves to fuel their upstream migrations (Mesa and Magie 2006; Cox and Heintz 2009; Hearsey and Kinziger 2015). Energetic status also differed among the four Alaska Chinook Salmon populations in this study. For example, fish sampled at the initial stages of their spawning migration at the mouth of the Yukon River had significantly higher lipid reserves than those sampled at the same stage in the Nushagak River (Figure 2.4). Populations of Chinook Salmon in the large Yukon River basin likely have higher energetic costs of migration owing to a longer, more arduous migration relative to populations in the smaller Nushagak River basin. When compared to estimates for populations collected at the beginning of their spawning migrations in Puget Sound and the Columbia, Sacramento, Skeena, and Fraser Rivers (mean total body lipids = 10.5%; O'Neill et al. 2014), our study indicates that total lipids of Chinook Salmon captured near western Alaska river mouths (Emmonak and Nushagak), were much higher (mean = 38.4%). This includes two fish for which proximate analysis estimated to have greater than 50% lipid content. These fish were both large females, measured at the mouth of the Yukon River, which may indicate that these fish need high energy stores to produce eggs and migrate far upstream to their spawning locations. The proximate composition estimates from this study will serve as benchmarks for future research to examine changes in Chinook Salmon energetic content that may be associated with changes in abundance for populations in Alaska and elsewhere.

The Whitman Hatchery population was expected to represent the mid-range of energetic status, between the populations sampled near the beginning (Emmonak and Nushagak), and at the end (Chena) of their spawning migrations. Interestingly, the Whitman Hatchery population had some of the lowest lipid content and highest water content compared to the other populations. The lower lipid content may be a result of their hatchery origin. Specifically, individuals may not need to have high energy storage requirements relative to wild origin fish that swim thousands of kilometers upstream to spawn (Haring et al. 2016). Chinook Salmon from Whitman Hatchery are also sourced from wild Chinook Salmon in the Chickamin River, a relatively short river compared to the Nushagak, Yukon or Stikine Rivers also used in this study, where fish may not have needed to store as much energy for their freshwater migrations as the salmon from larger river systems (Stopha 2016). This may also be due to inherent differences between sample locations or differences based on the time of year the population was sampled. The Whitman Hatchery population was sampled in mid-August and were the last group of fish to be sampled, potentially contributing to this population having the lowest energetic status, as fish have been shown to decrease in lipid content over the maturation period and can begin this maturation process while still in the ocean (Hearsey and Kinziger 2015). This provides evidence that Chinook Salmon use a majority of their lipid stores in their freshwater spawning migrations in systems with longer freshwater migrations and that fish with a shorter freshwater migration period use these stores to mature prior to entering the river system. This information highlights the importance of developing simple and non-lethal methods to accurately and precisely estimate proximate components of these populations.

In contrast to other studies that have indicated pronounced differences between male and female energy stores at the beginning of upstream migrations, when females have higher energy

stores than males (Idler and Clemens 1959; Crossin et al. 2004; Mesa and Maggie 2006; Hearsey and Kinziger 2015), we found no differences in lipid content between sexes. It is possible that we did not observe sex-based differences in lipid content because the populations used for this study were sampled over a short time period at each location and spawning stage. For example, Chena River and Whitman Hatchery fish were collected over one day each, while Nushagak River Chinook Salmon were caught over a three day time period. Thus the fish from the Nushagak River were most likely travelling to similar spawning locations, as individuals that enter the river at similar times are often from the same spawning tributary group (Eiler et al. 2015; Clark et al. 2015; Chapter 1), while Chena River and Whitman Hatchery individuals had reached their spawning location at similar times and thus expended comparable amounts of energy en route. This could be why we did not observe differences in energetic status between sexes, and may indicate that fish from similar spawning groups are expending comparable amounts of lipid and water reserves in their upstream migrations and egg maturation period regardless of sex (Quinn 2005).

BIA Model Development

The Q2 and CQR devices predicted water and lipid content better than the length and weight models alone, indicating that the use of BIA does improve upon previous methods of measuring energetic status for Chinook Salmon (e.g., condition indices). Also using BIA, we were able to develop a predictive model for energetic status in Chinook Salmon based on the thresholds suggested by Hartman et al. (2015) that indicated minimums of coefficient of determination value (R^2) of ≥ 0.8, sample size of > 60 fish, and a minimum lipid range of 29% are needed for a successful BIA predictive model. Based on these criteria, percent lipid and percent water models from the Q2 device electrical measurements were most successful and met

model validation criteria. While the same models developed for the CQR device outperformed models that contained only length and weight, their predictive ability was lower relative to Q2-based models.

The observed differences in model predictive performance from measurements between the two devices could be due to electrode placement and type. For example, the Q2 has needle electrodes that can be placed at variable lengths along the body with larger distances for longer fish, allowing the current to pass through more body tissues and collect a better sample of lipid content throughout the whole body. Moreover, we also used locations (DML and VTL) determined in a previous study to give the best representation of whole body tissue composition (Hafs and Hartman 2011). In contrast, the CQR device has rod electrodes that depress into the fish's body, as opposed to contacting the fish through needle punctures. The electrodes are at fixed locations thus may not be representative of whole body resistance and reactance values (Cox et al. 2011). Another factor influencing these differences could be that the Q2 device model contained BIA measurements from both the dorsal and ventral surfaces, whereas CQR measurements were taken on only the dorsal surface. Previous studies have found that dorsal and ventral surface BIA measurements combined provide a better representation of energetic status and predictive power in BIA models, and is suggested by the authors for using the device in the future (Hafs and Hartman 2011; Stolarski et al. 2014; Hartman et al. 2015). Though the CQR model had a lower coefficient of determination, the device is more portable and easier to use than the Q2, leading to less required training to use the device. This may be ideal for field applications, where fish need to be measured quickly and sampling gear needs to be minimized, but users will need to consider trade-offs in predictive precision between the two devices.

BIA Model Application

The ability to predict energetic status of similar species with one calibrated BIA model was tested in this study, and our findings indicate that models developed for a single species performed much better than using models interchangeably between two species (Chinook and Chum Salmon in this case), though combining Chinook and Chum Salmon data produced models comparable to the single species model. Though Chinook and Chum Salmon are similar in body shape, using the models interchangeably did not produce coefficients of determination above the model validation threshold, though they were close and may be useful in populations of Pacific Salmon that are in periods of reduced abundance or decline and if lethal sampling from these populations is not be possible (Groot and Margolis 1991; Hartman et al. 2015). The model developed using Chinook and Chum Salmon data together had comparable R^2 and RMSE values to the species-specific models. This could be an alternative method of creating species- specific models for sensitive populations, as individuals would not have to be removed from the population to calibrate a model.

The BIA model developed using the CQR device was applied to Chinook Salmon on the Stikine River to investigate differences in energetic status in relation to sex and spawning location. The CQR device was successfully implemented into an existing study capturing and tagging Chinook Salmon, and had little impact on the stock assessment activities and protocol. Measurements took approximately 30 seconds and fish showed no signs of stress or injury during or after the measurement process. The finding that there were no differences in model predicted percent lipid or water between sexes or among spawning locations in the Stikine River are consistent with the results from proximate analysis on fish from the other sample locations in Alaska. For example, Chinook Salmon that had been measured for energetic status using

proximate composition analysis from locations near the mouth of the river that would be similar to fish from the Stikine River (Emmonak and Nushagak) had between 26.36 and 51.02 % lipid and 49.26 and 68.61% water, while fish measured using BIA only from the Stikine River had between 9.51 and 41.45% lipid and between 59.28 and 78.58% water. The lower lipid content and higher water content in fish from the Stikine River may be due to the fact that fish swimming to spawning habitat in the Stikine River migrate shorter distances than those in the Yukon or Nushgak River systems. There may also be no differences in energetic status between sexes or among spawning locations because the Stikine River is a relatively short system, and fish may not need to adapt large energy stores for their spawning migrations.

Management Implications

This study provides a platform for future studies of energetic status in Chinook Salmon and other Pacific Salmon species, as well as the means to develop monitoring studies and determine energetic status levels in Chinook Salmon populations. Managers can use the results from this study to establish benchmark estimates of energetic status for Chinook Salmon populations over space and time; use of the BIA approach will allow this to be done non-lethally and quickly. From the four sampled populations used to derive laboratory estimates of lipid and water content, we determined that there are differences in energetic status among Chinook Salmon from different locations in Alaska. This is an important consideration for management, as an understanding of the differences in energetic status among populations could be used to develop more specialized management protocols for different locations. For example, if two nearby and similar river systems are determined to have very different levels of energetic status, the population with the lower energetic status may need to be monitored more to determine if low energetic status levels play a part in the declines and in order to ensure that fish will have the

ability to travel to their spawning stream and reproduce. Additionally, these body composition values determined using proximate composition analysis and BIA can be used as benchmarks for future studies to assess the effects of changes in ocean or river environments on energetics of these populations, which can be used to understand how levels that allow fish to successfully reproduce (Hartman and Margraf 2008).

More research should be conducted on Chinook Salmon energetic status, with samples from additional populations and life stages beyond those used in this study to determine if similar patterns in body composition exist between locations and across spawning stages (e.g., bright pre spawn, coloration/sexual dimorphism pre spawn, post-spawn). Monitoring energetic status across life stages and locations will be important for future management of Chinook Salmon, as we can now study how environmental and biological characteristics contribute to deviations from these values. Improved knowledge of the influence of the environment on energetic status of Chinook Salmon can provide more information for managers on how to regulate fisheries on the populations. Long term, consistent monitoring of energetic status could lead to a better understanding of the effects of climate change and habitat alterations to Chinook Salmon populations, and the BIA technique could easily be implemented into existing population monitoring studies.

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FIGURES AND TABLES

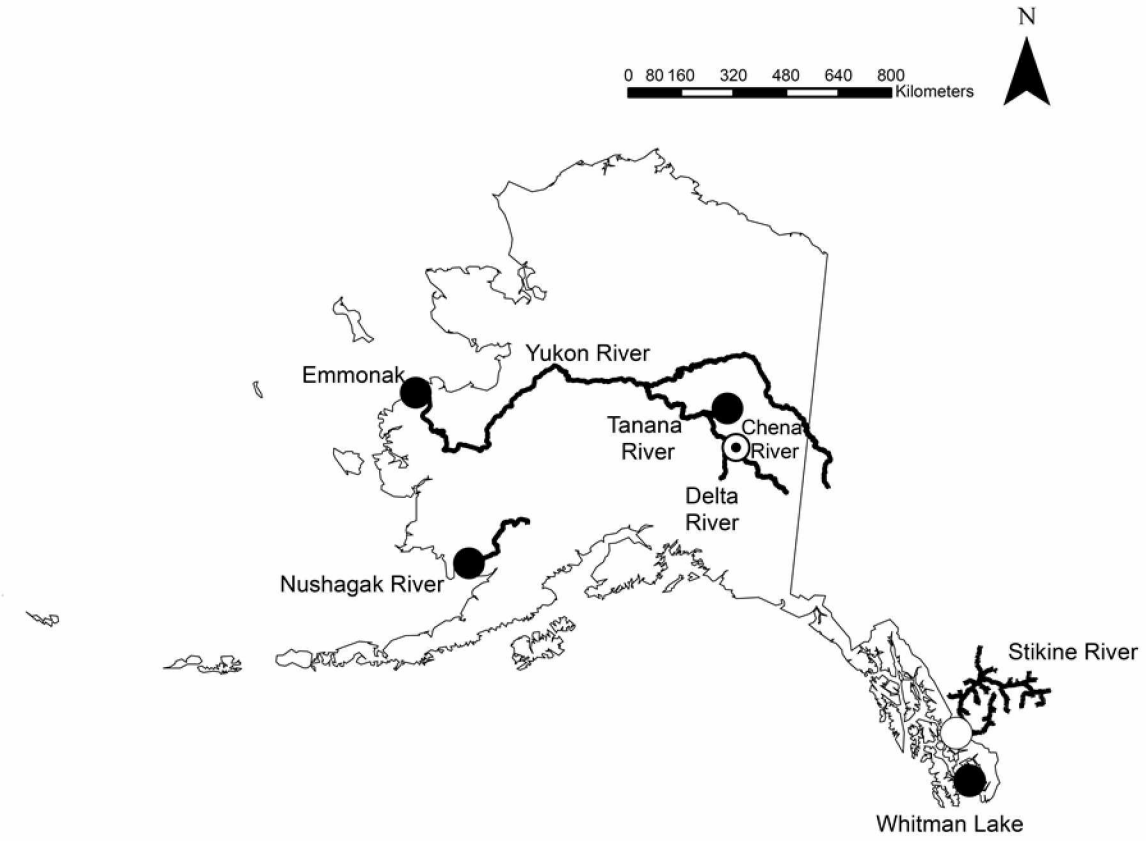

Figure 2. 1. Map of sites in Alaska where Chinook Salmon were sampled for proximate analysis and bioelectrical impedance analysis (BIA; filled circles) and BIA only (open circle). Chum Salmon were sampled for BIA and proximate analysis at Emmonak and the confluence of the Tanana and Delta Rivers (filled circle in open circle).

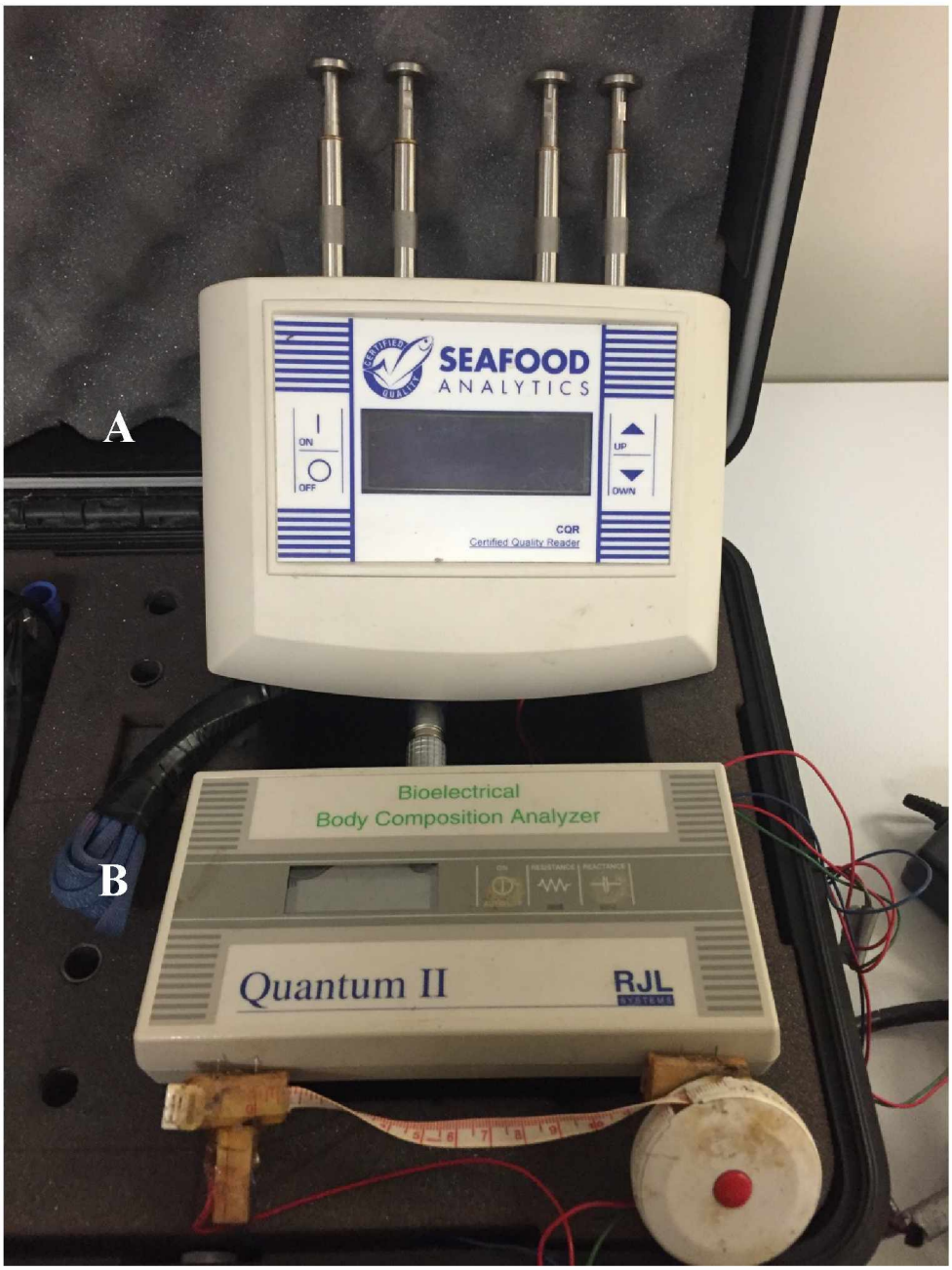

Figure 2. 2. Two devices used to measure electrical properties (resistance and reactance) of Chinook Salmon in the field. Seafood Analytics Certified Quality Reader (A) and RJL Systems Quantum II Bioelectrical Impedance Analysis meter (B).

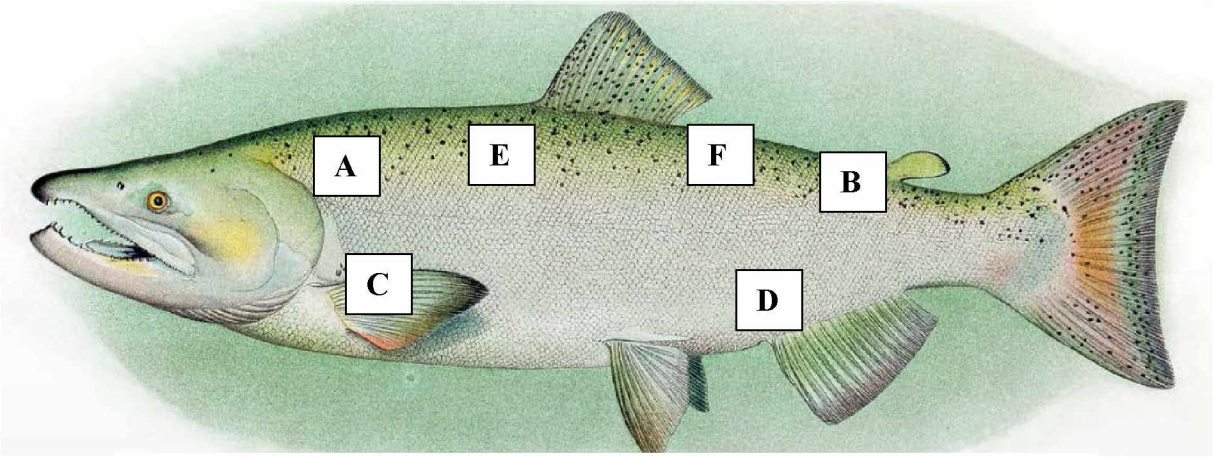

Figure 2. 3. Diagram of electrode placement for electrical measurements using the Quantum II device at dorsal midline (A and B) and ventral total length (C and D) locations, and using the Certified Quality Reader device placing the electrodes forward of the dorsal fin (E and F; Hafs and Hartman 2011).

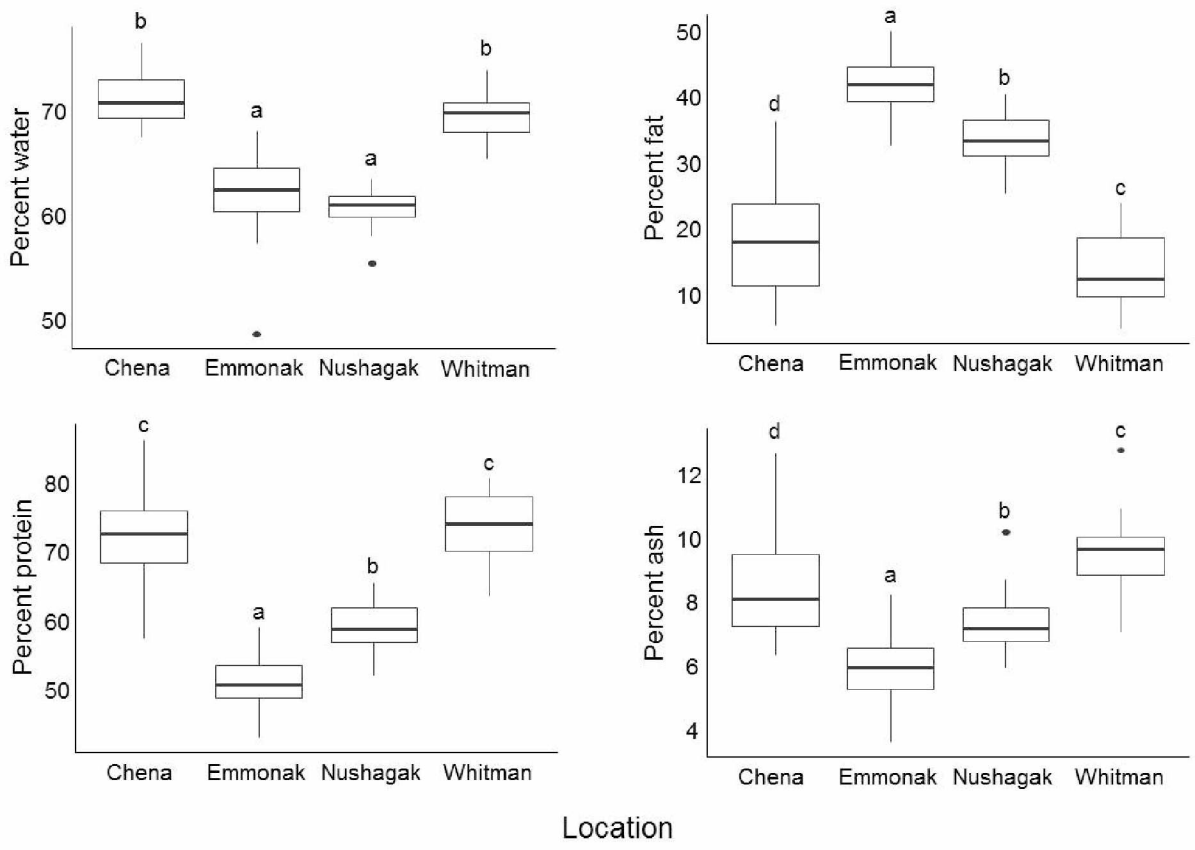

Figure 2. 4. Proximate composition (upper left = percent water; upper right = percent lipid; lower left = percent protein, and lower right = percent ash) of Chinook Salmon collected from four locations in Alaska. Letters above the boxplots indicate results of ANOVA and Tukey's post hoc HSD tests, letters that are the same indicate no statistically significant difference between means with an alpha < 0.05. The box dimensions represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles, the solid lines inside the boxes are the medians, and dots represent outliers.

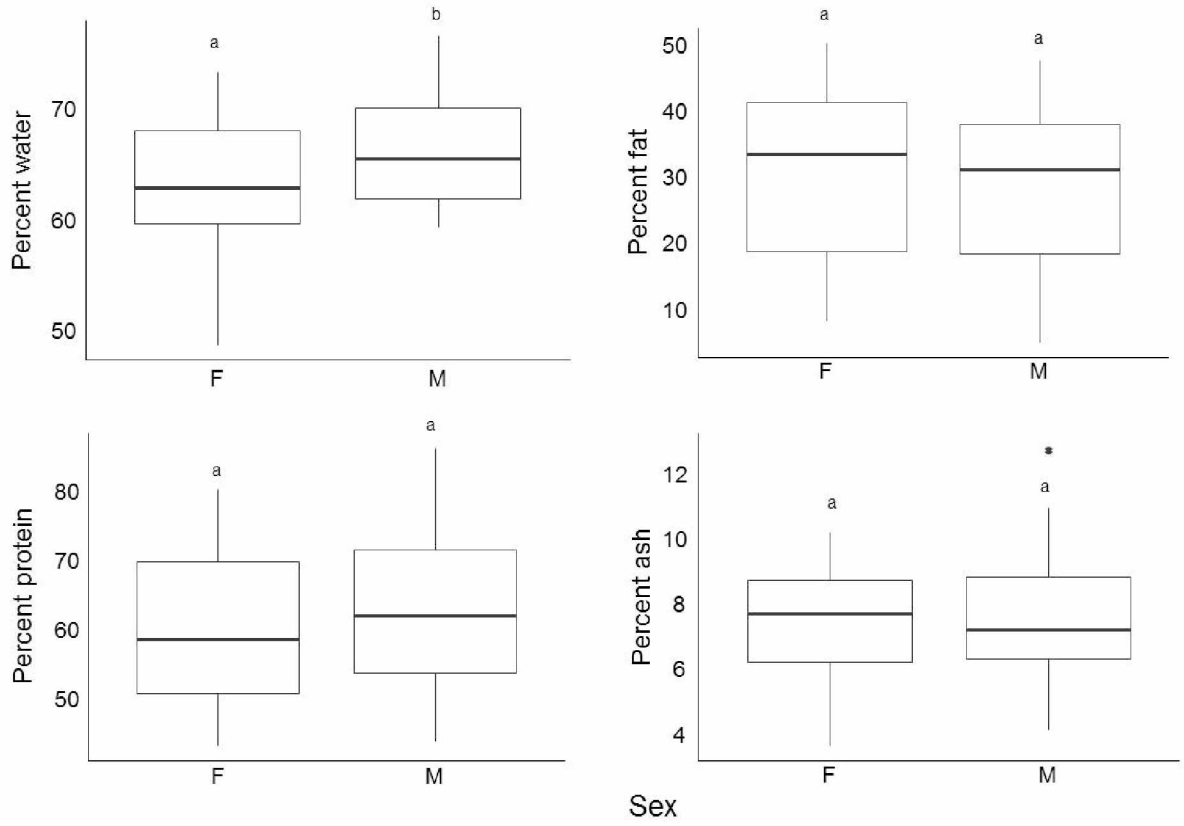

Figure 2. 5. Proximate composition of male and female Chinook Salmon (upper left = percent water; upper right = percent lipid; lower left = percent protein, and lower right = percent ash) compared between sexes (y-axis). Letters above the boxplots indicate results of ANOVA, letters that are the same indicate no statistically significant difference between means. The box dimensions represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles, the solid lines inside the boxes are the medians, and dots represent outliers.

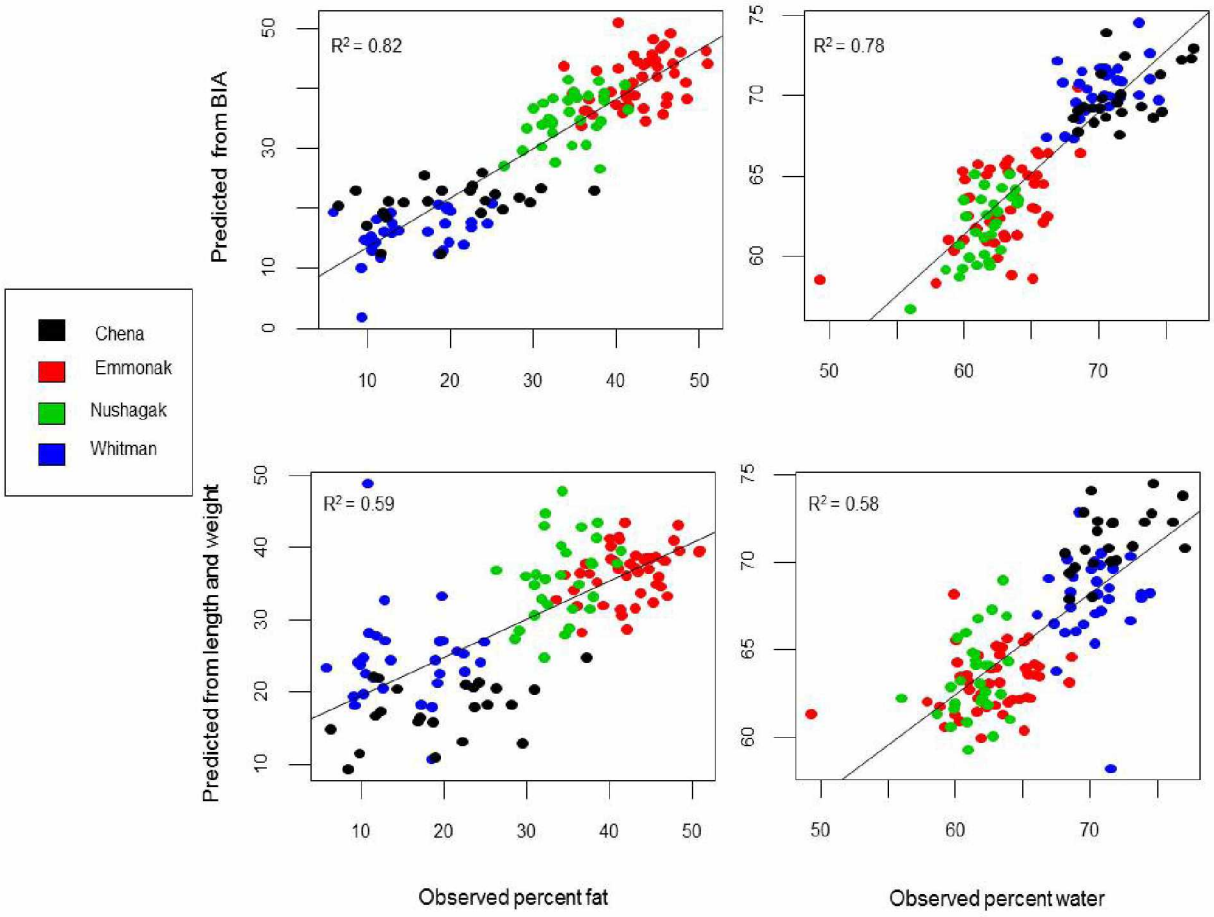

Figure 2. 6. BIA model predictions (top; upper left = percent lipid, upper right = percent water) and predictions from length, and weight regressions (bottom; lower left = percent lipid, lower right = percent water) for percent lipid and percent water against composition determined by proximate analysis (x-axis) for the Quantum II device. Colors indicate different sample locations.

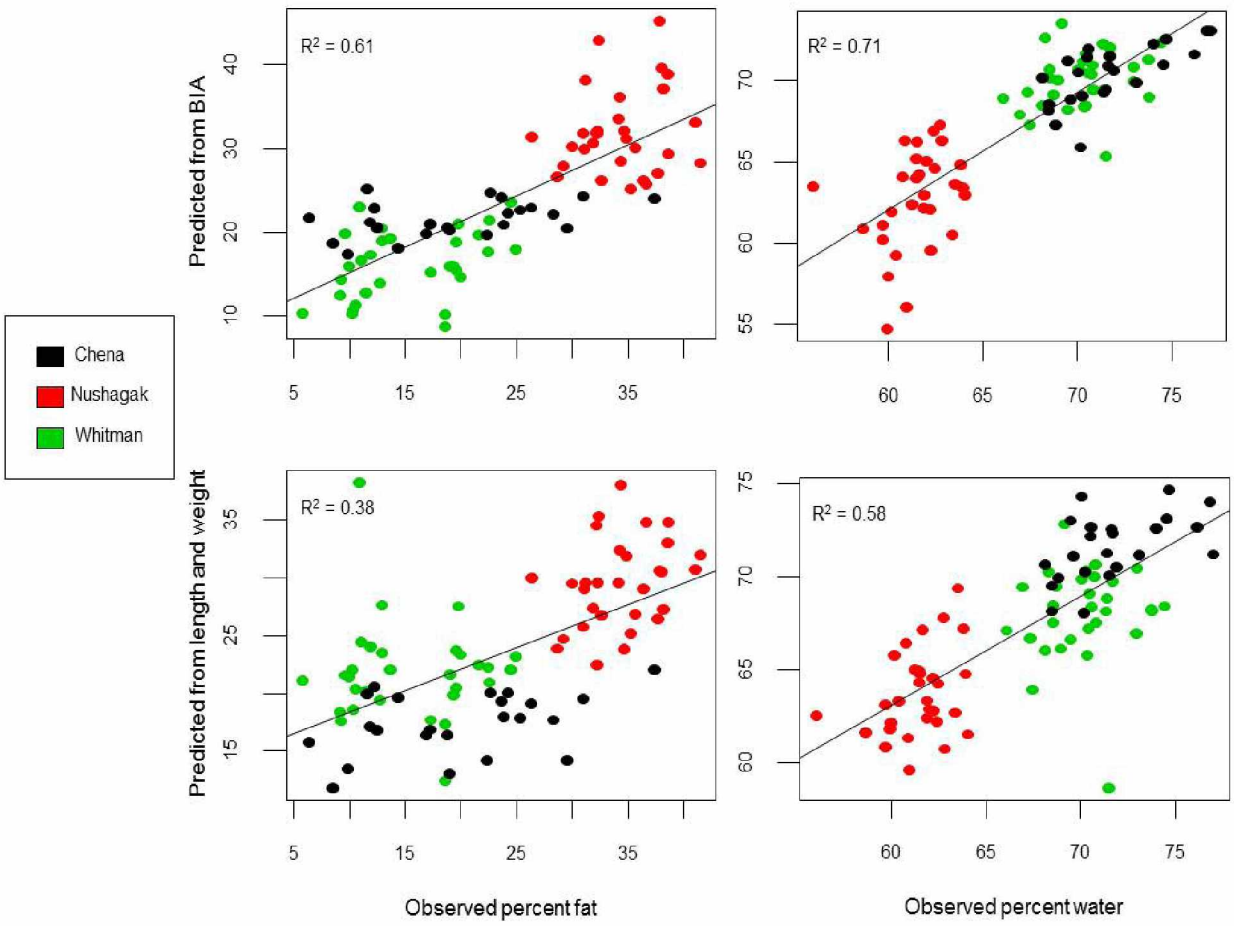

Figure 2. 7. BIA model predictions (top; upper left = percent lipid, upper right = percent water) and predictions from length, and weight regressions (bottom; lower left = percent lipid, lower right = percent water) for percent lipid and percent water against composition determined by proximate analysis (x-axis) for the Certified Quality Reader (CQR) device. Colors indicate different sample locations.

Table 2. 1. Electrical parameters from bioelectrical impedance analysis measurements using the Quantum II (Q2) and Certified Quality Reader (CQR) devices used in model development to predict energetic status of Chinook Salmon. DL = detector length (mm), x = reactance (Ohms), r = resistance (Ohms).

Parameter	Symbol	Units	Equation
Reactance	*X*	Ohms	Measured by Q2 and CQR analyzer
Resistance	*R*	Ohms	Measured by Q2 and CQR analyzer
Reactance in parallel	*Xcp*	Ohms	$DL^2/(x + (r^2/x))$
Resistance in parallel	*Rp*	Ohms	$DL^2/(x + (r^2/x))$
Impedance in parallel	*Zp*	Ohms	$DL^2/(r \cdot x/(r^2 + x^2)^{0.5})$
Reactance in series	*Xc*	Ohms	DL^2/x
Resistance in series	*Rs*	Ohms	DL^2/r
Impedance in series	*Zs*	Ohms	$DL^2/(r^2 + x^2)^{0.5}$
Phase angle	PA	Degrees	$\text{Arctan}(x/r) \cdot 180/\pi$
Standardized phase angle	DLPA	Degrees	$DL \cdot (\arctan(x/r) \cdot 180/\pi)$
Length	len	mm	NA
Weight	wt	kg	NA

Table 2. 2. Number of Chinook Salmon sampled for proximate composition analysis and bioelectrical impedance analysis model development (N) by location and sex (M/F). Means and standard deviations for fork length (FL; mm), weight (WT; kg), percent lipid and percent water are shown.

Location	N	M	F	Mean FL	Mean Wt	Mean %Lipid	Mean %Water
Chena	23	21	2	733.0 ± 82.2	4.11 ± 1.6	19.71 ± 8.07	71.69 ± 2.69
Whitman	30	15	15	820.0 ± 64.4	6.27 ± 1.6	15.33 ± 5.36	70.19 ± 2.11
Nushagak	30	17	13	810.6 ± 98.8	7.30 ± 2.53	33.48 ± 3.68	61.44 ± 1.69
Emmonak	46	27	19	803.2 ± 112.6	7.28 ± 2.84	42.56 ± 4.17	62.71 ± 3.19

Table 2. 3. Summary of BIA models used to predict water and lipid content in Chinook Salmon using the Quantum II and CQR devices including the number of model parameters (K), Akaike information criterion (AIC_c), coefficient of determination (R^2) and root mean squared error (RMSE). Models were developed from 1) lateral and ventral combined BIA data sets, 2) lateral data only, 3) ventral data only, and 4) length and weight data. CQR device measurements were taken on the lateral surface only.

Device	Component	Data Set	K	AIC_c	R^2	RMSE
Q2 Device						
	Water	Combined	10	593.4	0.78	2.43
		Lateral	9	674.5	0.56	3.30
		Ventral	10	662.1	0.61	3.17
		Length and Weight	4	657.9	0.58	
	Lipid	Combined	9	788.6	0.82	5.33
		Lateral	10	826.8	0.76	6.05
		Ventral	11	843.1	0.73	6.40
		Length and Weight	4	902.9	0.59	
CQR Device						
	Water	Combined	13	429.3	0.71	2.66
		Length and Weight	4	439.5	0.58	
	Lipid	Combined	13	571.6	0.61	6.27
		Length and Weight	4	588.9	0.38	

Table 2. 4. Model coefficients and standard errors (in parenthesis) for the top predictive BIA model (Table 2.2) for water and lipid content developed by lateral and ventral combined data sets. Model developed with BIA data collected using the Quantum II device. Blank cells indicate that the variable was not included in the top model.

Variable Set	Variable	Water	Lipid
	Intercept	84.7467 (1.5761)	22.1664 (6.3050)
Biological	Fork Length		-0.0427 (0.0095)
	Weight	-0.5608 (0.2308)	
	Resistance in Parallel		0.0383 (0.0028)
Lateral	Impedance in Parallel	-0.0032 (0.0005)	
	Capacitance	7.8-e26 (0.000)	
	Reactance in Parallel	0.0930 (0.0388)	
	Resistance in Parallel	-0.5760 (0.1834)	1.3275 (0.3042)
Ventral	Impedance in Parallel		-0.0004 (0.0002)
	Impedance in Series	0.5811 (0.1851)	-1.3674 (0.2993)
	Capacitance	-1.59-e26 (0.000)	1.56-e25 (0.000)
	Standardized Phase Angle	-0.0063 (0.0006)	0.0099 (0.0014)

Table 2. 5. Model coefficients and standard errors (in parenthesis) for the top predictive BIA model (Table 2.2) for water and lipid content developed with BIA data collected using the CQR device. Blank cells indicate that the variable was not included in the top model.

Variable Set	Variable	Water	Lipid
	Intercept	17.6975 (-15.5931)	115.5685 (-36.7515)
Biological	Fork Length	0.0525 (-0.0116)	-0.0959 (-0.0273)
	Weight	-1.5281 (-0.7240)	2.8004 (-1.7063)
	Body Mass Index	-0.0209 (-0.0075)	0.0326 (-0..0177)
Electrical	Reactance in Parallel	8.0703 (-7.6689)	-11.7362 (-18.0748)
	Reactance in Series	909.9931 (-871.5416)	-1522.7540 (-2054.1430)
	Resistance in Parallel	-41.3376 (-34.9375)	117.6620 (-82.3445)
	Resistance in Series	818.8484 (-793.7104)	-1285.6570 (-1870.7020)
	Impedance in Parallel	-646.8353 (-621.3633)	1113.8360 (-1464.4960)
	Impedance in Series	-852.1781 (-833.3435)	1279.5750 (-1964.1140)
	Capacitance	3.8498+e20 (-1.4459+e20)	-1.0588+e21 (-3.4079+e20)
	Phase Angle	-0.0781 (-0.5974)	0.5480 (-1.4081)

Table 2. 6. Coefficient of determination (R^2) values and root mean squared error (RMSE) for bioelectrical impedance analysis (BIA) models from Chinook and Chum Salmon measured using the Quantum 2 device with 1) Chum Salmon model parameters to predict Chinook Salmon energetic status, 2) Chinook Salmon model parameters (Table 2.4) to predict Chum Salmon energetic status, 3) using Chum Salmon model parameters to predict Chum Salmon energetic status, 4) Chinook Salmon model to predict Chinook Salmon energetic status, and 5) Chinook and Chum Salmon combined data Chinook Salmon model R^2 and RMSE values used for comparison are in Table 2.3.

Model	Data	R^2	RMSE
Lipid			
	Chinook from Chum	0.53	19.47
	Chum from Chinook	0.63	7.69
	Chum only	0.93	3.21
	Chinook only	0.78	2.43
	Chinook and Chum	0.84	4.99
Water			
	Chinook from Chum	0.18	12.08
	Chum from Chinook	0.52	3.91
	Chum only	0.84	2.24
	Chinook only	0.82	5.33
	Chinook and Chum	0.81	2.48

General Conclusions

This study examined migration behaviors (migration timing and rates) and energetic status of Chinook Salmon across multiple habitats and stages of spawning migrations in Alaska. Migration behaviors were determined using radio telemetry in two Southeast Alaska transboundary rivers, both of which are key Chinook Salmon stocks in Alaska and British Columbia. Energetic status was determined for Chinook Salmon from four populations in Alaska that represented early and late stage spawning migrations. From the sampled Chinook Salmon, a non-lethal model using bioelectrical impedance analysis (BIA) was created that can be used to predict energetic status in other Chinook Salmon populations. The key results of this study were:

- Spawning locations were determined for a total of 673 Chinook Salmon from the Stikine (N = 270) and Taku (N = 403) rivers in 2015 and 2016. In the Stikine River, most fish had a final location in the Tahltan River (49%), followed by the Chutine River, Verret River, Christina Creek, Iskut River and finally, Andrew Creek. In the Taku River 47% of the tagged salmon were located in the Nakina River, followed by the Nahlin River, Dudidontu River, Kowatua River, Inklin River and the Sloko River.
- Migration timing for Chinook Salmon tracked to spawning locations farther upstream was earlier than those with more downstream spawning locations, and migration timing was earlier in the Taku River than in the Stikine River (Stikine = 9 June ± 15 days, Taku = 1 June ± 12 days).
- Chinook Salmon migration rates decreased with increasing discharge, fish that spawned farther upstream had faster migration rates than those that spawned in the lower river, migration rates decreased over time as fish swam farther upstream, and rates were slower for fish from the Taku River and in 2016.

- Migrating Chinook Salmon sampled at a river's mouth (ANOVA: $F = 202.1$, df = 3, $P<0.001$; Emmonak = 42.56 ± 4.17, Nushagak = 33.48 ± 3.68) had higher total body lipid (%) compared to those sampled near their spawning grounds (Chena = 19.71 ± 8.07, Whitman = 15.33 ± 5.36). Total body lipid did not differ between sexes ($F = 0.61$, df = 2, $P = 0.44$).
- Electrical measurements (resistance and reactance) taken with the Quantum II (Q2) BIA device explained 82 and 78% of the variation in total body lipid (%) and water content (%), respectively. The lipid and water BIA models were precise (based on root mean square error) to within 5.3 and 2.4%, respectively.
- The Q2 device explained more variation than the Certified Quality Reader (CQR) device for predicted total body lipid and total body water (CQR: 61% and 71% respectively), but the CQR device outperformed length and weight regressions alone for total body lipid (58%) and water (38%).
- The Chinook Salmon BIA model was less accurate when used to predict Chum Salmon energetic status (lipid: $R^2 = 0.63$, water: $R^2 = 0.52$), and vice versa (lipid: $R^2 = 0.53$, water: $R^2 = 0.18$) relative to Chinook and Chum Salmon-specific models (all $R^2 \geq 0.78$).
- I successfully used the CQR BIA device to estimate total body lipid (mean: 20.62%, range: 9.51 - 41.45%) and water (mean: 73.72%, range: 61.82 – 78.58%) of Chinook Salmon ($N = 127$) for the Stikine River population. I found no relationship between the predicted percent lipid and sex (ANOVA: $F = 0.27$, df = 1, $P = 0.61$) or spawning location ($F = 1.38$, df = 5, $P = 0.24$) and no relationship between predicted water content when compared to sex ($F = 0.29$, df = 1, $P = 0.59$) or spawning location ($F = 0.52$, df = 1, $P = 0.76$).

In the first chapter, migration timing and migration rates were studied to better understand the effects of environmental and biological factors on Chinook Salmon in two important Southeast Alaska and British Columbia rivers. The Stikine and Taku Rivers are the two largest producers of Chinook Salmon in the region, they provide important fisheries resources for Alaskan and Canadian user groups, and both are currently experiencing population declines (ADF&G 2013). In Southeast Alaska, climate change is expected to increase water temperatures and variability in discharge, environmental characteristics that are known to impact upstream migration behaviors in adult Chinook Salmon (Keefer et al. 2004; Keefer et al. 2015; Kovach et al. 2015; Chapter 1). Determining benchmark estimates of migration timing and rates in these two populations provides future researchers current migration characteristics against which to make future comparisons, and gives researchers an idea of the degree of impact that environmental and biological factors have on the migration characteristics of these populations. In this study, environmental factors, such as discharge and spawning location, were shown to have a significant impact on migration behaviors, while no significant impacts were found from the biological factors sex or length. Knowledge that environmental factors have more influence on Chinook Salmon migration behavior is valuable for managers in order to understand how to direct management resources. For example, if higher discharge rates are associated with a slower migration rate for Chinook Salmon travelling upstream to spawn, fish that are located in the Canadian in-river commercial fishing areas of the Stikine and Taku Rivers during periods of high discharge may be subjected to a higher degree of fishing pressure and harvest. Managers could then change the allowable fishing period to spread out the probability of an individual being caught. This information allows resource managers to approach in season management strategies with a more comprehensive view of fish behavior.

There is also concern about alterations to river habitat and water quality for Chinook Salmon and other salmonid species returning to these rivers due to the increasing prevalence of mining activity (Ream and Merriam 2017). Acid mine drainage, one of the most common environmental impacts from mining activities, leaches heavy metals into the aquatic habitat. Some heavy metals (e.g. copper, zinc) have been found to adversely impact migrating salmonids through damaging their olfactory system, which provides some of the mechanisms that help fish locate their spawning streams and avoid predators (Saunders and Sprague 1967; Baldwin et al. 2003; McIntyre et al. 2012). Studies have been conducted to assess the heavy metal content of fish near one of these mining locations in the Taku River, and concluded that currently, there are no differences in the heavy metal concentration in fish based on their proximity to acid mine drainage locations (Legere and Timothy 2016). Continuing to monitor both heavy metal content and migratory patterns of fish in these rivers, as well as correlations between them, can lead to a better understanding of how mines may be impacting these fish populations. Many mines in these river systems are still in the exploration stage (Clarke et al. 2016), and it will be important to study behavioral characteristics of fish species in these areas to be able to understand how they may be affected from habitat alteration or degradation of water quality.

The use of telemetry in this study as a means to determine distribution and migration behaviors of Chinook Salmon in the Stikine and Taku Rivers proved to be a useful method. Telemetry methods provide a powerful tool to collect data in remote locations (Adams et al. 2012), and much of the drainage area in the Stikine and Taku Rivers is accessible only by boat or plane. Stationary telemetry towers allowed continuous collection of data at multiple locations throughout the river basin with minimal time invested for set up and maintenance. Aerial surveys worked well to precisely determine spawning locations, and flight logistics were manageable due

to the nearby location of communities to the Taku and Stikine Rivers. Thus allowed me to survey large portions of the basin without stopping for fuel and allowed for the ability to change plans quickly if weather conditions did not allow a flight that day. Set up, maintenance and protocol for telemetry equipment and tagging fish did require training, though once the process was learned it was easy to reproduce and to teach to others. The telemetry data collected in this study can also be used for many other research applications, such as determining how many fish leave the river system after tagging (i.e., dropout rate; Richards et al. 2015a, 2015b), a more detailed look a pre-spawn mortality or tag induced behaviors, and differences in the timing of spawning for fish within different tributaries.

In the second chapter, I examined Chinook Salmon energetic status in four different populations across Alaska, developed a bioelectrical impedance analysis (BIA) model for the species, and assessed the applicability of this model to a more generalized BIA model and a remote tagging study. The lipid content in upstream migrating salmon is important to consider, as fish use these reserves as energetic fuel while on their way to their spawning grounds (Brett 1995). Salmon deplete most of these energy reserves as they migrate upstream and mature to spawn, and if have they are lacking sufficient lipid reserves at the onset of their migration, they may die before they reach their spawning location and thus will not be able to reproduce (Crossin et al. 2004; Mesa and Magie 2006; Minke-Martin 2017). I found that there were among-population differences in fish that were sampled for proximate analysis, and that this change in energetic status was based on whether fish were in the initial or final stages of their spawning migrations. The BIA model also proved useful and applicable to predicting energetic status of fish accurately and quickly (Cox and Hartman 2005; Hafs and Hartman 2011; Hartman et al. 2015).

To be consistent with previous research (Margraf et al. 2005; Hartman et al. 2015), the proximate analysis component of this research was conducted at the University of Idaho, Hagerman Fish Culture Experiment Station though it was originally intended to be completed at UAF. Hagerman Fish Culture Experiment Station personnel had the training and equipment to perform these analyses quickly. Moreover, having the samples analyzed from this research lab allowed me to include the Chinook Salmon sampled from Emmonak (Margraf et al. 2005) into this study, and make comparisons with Chum Salmon (Hartman et al. 2015). However, sending these samples to an outside source was likely more expensive than performing the analyses at UAF.

I compared multiple aspects of performance of resistance and reactance measurements taken using the Quantum II (Q2) and Certified Quality Reader (CQR) devices to estimate energetic status of Chinook Salmon. Although estimates from the Q2 model were more precise than those made with the CQR device, BIA model results from the latter still outperformed models based solely on fish length and weight. Moreover, I found that the CQR device to be more portable and easier to use in the field because it is more compact, does not have long wire components, does not use needle electrodes that need to penetrate into muscle flesh, and did not require extensive training. Thus the decision on which device to use will depend on study objectives and the acceptable amount of error. For example, a study in a remote location that is often performed in inclement weather may be better suited to the CQR due to the increased portability and fast assessment time. The Q2 may work better for an assessment of fish from a hatchery, as there are more facilities to handle fish and they are likely to be sedated during the process. Either device would make an excellent addition to monitoring programs. The ability to non-lethally and accurately estimate energetic status for declining Chinook Salmon populations

should be taken advantage of in monitoring studies, where we can now assess energetic status over multiple years and compare populations easily and effectively.

The ability to measure energetic status using BIA in conjunction with other ongoing studies, like the telemetry project from this research, can provide fisheries scientists with the means to develop more accurate estimates of energetic status for Chinook Salmon populations. These condition indices can then be compared throughout their range and related to environmental and biological characteristics. By using BIA to assess multiple populations over time, benchmarks for energetic status can be developed. This would provide researchers with knowledge about how populations change over time, what energetic content is required for survival, how this influences pre-spawn mortality, and could shed light on the effect of environmental conditions, whether in the marine or freshwater habitat, on energetic status. Future studies focused on determining how energetic status and the related environmental conditions influence pre-spawn mortality in Chinook Salmon may be particularly useful for researchers. Knowledge of energetic status levels in both the marine and freshwater environments for maturing and migrating Chinook Salmon could provide researchers with an idea of what conditions increase and decrease energetic status, and whether adults returning from the ocean have levels lower than the benchmark estimates determined for successful spawning. This information can help determine how variation in energetic status may be contributing to the declines in Chinook Salmon populations.

In conclusion, this study quantified the relative influence of physical and biological characteristics on Chinook Salmon migration behaviors, provided evidence that energetic status in Alaska Chinook Salmon populations differs based on their location, and developed a new model to precisely and non-lethally predict energetic status for the species. The findings from

this study can be used to further understand migration characteristics in salmon, whether as a range-wide comparison of Pacific Salmon migrations, as a benchmark for Chinook Salmon in Alaska or comparisons within the Stikine and Taku Rivers specifically. The use of BIA as a tool to monitor energetic status in Chinook Salmon quickly, inexpensively, and non-lethally, whether over time or among different populations, may be useful for managers to understand how energetic status is influenced by environmental conditions, fish morphology, behaviors and population abundance. This study contributes knowledge that adds new information and methods to the field of fisheries research and can be used to develop more informed management strategies and future research projects.

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Appendix

Appendix A. Telemetry 2016 IACUC approval

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UAF UNIVERSITY OF ALASKA FAIRBANKS

hal Animal Care and Use Committee — Institutional Animal Care and Use Committee

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909 N Koyukuk D

March 14, 2016

To: Jeff Falke
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [878398-2] Stikine River Chinook Salmon Telemetry

y Administrative Review: The IACUC reviewed and approved the Revision of Personnel List referenced above b

14, 2016	Received:	March
14, 2016	Approval Date:	March
14, 2016	Initial Approval Date:	March

Expiration Date: March 14, 2017

is action is included on the April 14, 2016 IACUC Agenda. Th

otocol approved by Full Committee at the last meeting. Pr

PI responsibilities:

s protocol.
nd could

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol a result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit mc 006 "Significant changes requiring IACUC revie*
- *Inform research personnel that only activities de performed. Ensure personnel have been approp*

difications to the IACUC when necessary (see form
v" in the IRBNet Forms and Templates)

scribed in the approved IACUC protocol can be
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tted to the IACUC previously.

e animal research personnel are aware of the reporting procedures on the following page.

- *Be aw the dc subm*
- *Ensur*

Appendix B. BIA 2016 IACUC approval

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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 23, 2016

To: Jeff Falke
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [905630-2] Development and calibration of bioelectrical impedance analysis as a measure of energetic status of Chinook salmon (Oncorhynchus tshawytscha)

The IACUC reviewed and approved the Response/Follow-Up referenced above by Designated Member Review.

Received:	May 18, 2016
Approval Date:	May 23, 2016
Initial Approval Date:	May 23, 2016
Expiration Date:	May 23, 2017

This action is included on the June 9, 2016 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*